



UNIT 25 ECOLOGY

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HABITAT

PHYSICO-CHEMICAL FACTORS

COMMUNITY

BIOTIC FACTORS

STUDY GUIDE

This Unit consists of three components: the text, an experiment and a TV programme 'Rabbits and chalk grasslands'. Colour Plates 3–14 are referred to in the text, and you will find them at the back of this binding.

The experiment, to estimate k -values for the holly leaf miner, *Phytomyza illicis*, in Section 4.4, is an important part of the Unit. To do the experiment you will need to have a supply of mined holly leaves. So look ahead to this Section *now*, before you start the Unit, in order to ensure that you are ready to do the experiment when you come to it. The experiment takes about two hours, excluding the time taken to collect the leaves.

You will derive most benefit from the TV programme if you have read Sections 1 and 5 before you view it.

I INTRODUCTION: ECOSYSTEMS, COMMUNITIES AND POPULATIONS

In the last three Units you have learned about the processes that go on inside living organisms: about the chemicals involved; about how organisms synthesize and break down chemical substances in their bodies, obtain energy, and make proteins; about how the physiological systems inside the body work, and so on. In this Unit we return to the perspective we adopted in Unit 19: that of the whole organism. In Unit 19 we showed how important it is to consider the success or otherwise with which an organism copes with the demands of life—how fit it is, in the Darwinian sense. In this Unit we look in more detail at what these demands are, bearing in mind the knowledge that you now have about the physiological and biochemical processes that take place inside organisms. In summary, we are going to ask how organisms fare in their environment—that is, in the world round about them.

We call the environment in which an individual animal or plant normally lives its **habitat**. Any habitat has certain distinctive features: a particular climate, a particular kind of soil, a particular kind of water—either marine or freshwater, running or still—and so on. Features of this kind that influence an organism are termed the **physico-chemical factors** of its habitat. Other organisms living in the same place also constitute an important part of the habitat.

☐ In what kind of habitat are bluebells found, and what other organisms dominate this kind of habitat?

☒ Bluebells are found in deciduous woods where, of course, trees are a significant part of the habitat.

The organisms that share a habitat are important to each other because one may eat the other, they may compete with each other for food, or one may provide shelter for the other. Collectively, the organisms make up the biotic **community** of that habitat and provide the **biotic factors** operating in it. A full description of an organism's habitat involves a description of the physico-chemical and biotic factors that apply there.

Biotic and physico-chemical factors are not independent of one another, of course. The trees in a wood affect the humidity, temperature and illumination there, and so influence the physico-chemical features of the environment for animals and plants within the wood, including their own offspring (seedlings). Conversely, a particular set of physico-chemical factors, such as a prevailing harsh wind blowing off the sea, a cold climate and rocky ground, affect which kinds of organisms can live there. The organisms that come to share the same place in this way constitute part of each other's habitat.

PHYTOPLANKTON

ZOOPLANKTON

ECOSYSTEM

ECOLOGY

POPULATION

It is common knowledge that organisms are selective about where they live—some more so than others. Gardeners are familiar with ‘lime-hating’ and ‘lime-tolerant’ plants. Bluebells, which are such a common sight in the deciduous woods of Britain, are a rarity in most of continental Europe. The malarial parasite, *Plasmodium*, that you met in Unit 21 can multiply in mammalian blood cells and, at another stage of its life cycle, only in certain species of mosquito. The koala bear eats leaves only from certain species of *Eucalyptus*; both koalas and *Eucalyptus* trees occur naturally only in Australia. By contrast, there are a number of species that are very widely distributed; for example, bracken fern, *Pteridium aquilinum*, the common reed, *Phragmites australis*, the starling, *Sturnus vulgaris*, and the house mouse, *Mus musculus*. Some of these organisms are illustrated in Plate 3 (in the Plate section at the end of this binding).

Because organisms are selective about where they live, those that share the same requirements or tolerances live in the same kinds of habitat. On rocky shores around Britain you will find seaweeds, crabs, limpets, herring gulls and mussels. Although they share the same habitat, each of these species has its own distinctive way of life. For example, you may think that mussels and limpets have a lot in common, but mussels are firmly attached to rocks and filter seawater for food while limpets move around when covered by the sea and graze algae from the surface of rocks. These organisms form part of the rocky shore community. The community on rocks exposed to strong wave action is different to the community of a sheltered shore, and both are different to the community of a sandy shore. It is sometimes useful to think of communities as subdivided according to types of organisms into, for example, a seaweed community, a crab community and a bird community. So, the term ‘community’ can be used to refer to the whole collection of organisms of all types in a habitat—that is, the biotic community—or to a particular group, e.g. the plant community or bird community, or even to just that part of the insect community found living on the leaves of an oak tree.

- ☐ Figure 1 shows a collection of organisms in a freshwater pond. What communities can you see in this habitat and what organisms belong to them?

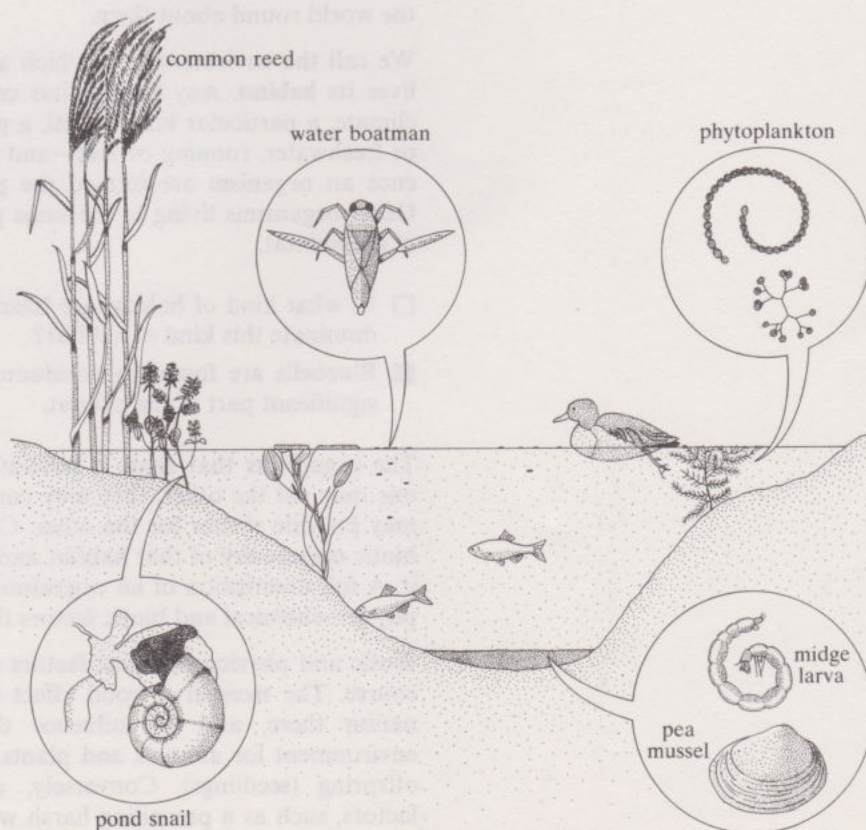


FIGURE 1 A freshwater ecosystem: a community of organisms living in a pond habitat.

■ The biotic community of the pond can be divided into smaller communities belonging to the more limited habitats within the pond habitat. These include the communities of the open water (the plankton and the fish), of the shallow water at the edge of the pond (the rooted plants and their associated animals), of the muddy bottom (many bacteria and also burrowing animals such as mussels and midge larvae) and of the water surface (water boatmen). Another way of dividing up the communities is according to the types of organism present, such as minute open-water plants (**phytoplankton**), small open-water animals (**zooplankton**), fishes, rooted plants, insects living among the rooted plants, and molluscs (snails and mussels).

□ What is the difference between a *habitat* and a *community*?

■ A habitat is like the address of an organism; the community is the collection of neighbours (a diverse assemblage but some of them related species with the same family name) who are found near that address.

Habitats are rarely isolated from each other. For example, a wood may have a stream flowing through it, and animals in the stream may live on dead leaves and other material falling into it from the trees.

□ How many habitats are there here?

■ At least two: the woodland habitat and the stream habitat. If the stream fed a pond, this would constitute another habitat.

To take account of the important links between habitats—upon which some of the communities in habitats depend for their living—we talk of an **ecosystem**. An ecosystem is a unit comprising *several* habitats and their communities of organisms, so it includes both the physico-chemical and biotic components. The best way to think of an ecosystem is as a network of habitats and communities linked by flows of energy and nutrients between them.

Ecosystems do not have visible boundaries around them, which you could see drawn on a map. The ecosystem is a *concept* that ecologists have come up with because it is a convenient way of describing the links between organisms.

The woodland ecosystem itself is part of a larger terrestrial ecosystem, perhaps a lowland area, which in turn is part of the island ecosystem of Britain. Even this island ecosystem is not a unit independent of all others: birds and butterflies and other less conspicuous organisms, as well as people, can move into or out of neighbouring continental areas. So whenever discussing and comparing ecosystems and communities, it is important to define them carefully.

This Unit is about ecosystems, habitats, populations and communities. They form the subject matter of the branch of biology called **ecology**, which is the study of the interaction of organisms with each other and with their environment. This large subject raises many fascinating and important questions. Here there is space to consider only a few of them. We take the ecosystem as our starting point, and ask how the organisms within a particular ecosystem interact with one another. Since they share the same environment, they are likely to have a profound impact on one another. For example, an organism may eat or be eaten by another organism in the same habitat. Organisms that are eaten (the prey) supply the energetic and chemical needs of those that eat them (the predators)—as you saw in Unit 22. Additionally, the *numbers* of each species in the community are, of course, affected by individuals eating or being eaten. A number of individuals of a species found in the same place is described collectively as a **population**.

To sum up: interactions between organisms result in transfers of energy and chemicals between them, and in numerical changes in population size. These are the topics of Sections 2, 3 and 4 of this Unit. Following from this

PRODUCTION ECOLOGY

PRIMARY PRODUCER

we go on, in Section 5, to look at communities, and how these may change with time. The impact of humans upon ecosystems is so pervasive that we bring this aspect of ecology into the discussion several times in the Unit.

SUMMARY OF SECTION 1

- 1 *Ecology* is the study of the interaction of organisms with each other and with their environment.
- 2 The place where an organism lives is its *habitat*. The description of a habitat should be based on its physico-chemical features and its biotic nature.
- 3 The organisms that live in a habitat make up the *biotic community*. The biotic community can be divided into smaller communities, consisting of organisms that share part of the habitat or a particular way of life, for example.
- 4 The best way to think of an *ecosystem* is as a network of habitats and communities linked by flows of energy and nutrients between them.

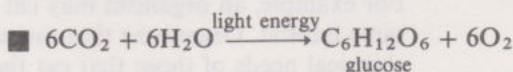
SAQ 1 Fill in each of the blanks in the following sentences using the appropriate term: community, ecosystem(s), habitat(s) or population(s).

- (a) A moorland contains grassland, scrub and stream
- (b) Highland streams are a for trout and salmon.
- (c) A domestic cat harbours a of fleas, *Ctenocephalides felis*, in its fur.
- (d) Ladybirds are members of the predator that feeds upon of greenfly, reducing their numbers.
- (e) The grassland of the Serengeti in Africa is grazed by a of large herbivores including wildebeeste, zebra, topi and buffalo.

2 ECOSYSTEMS AND PRODUCTION ECOLOGY

Production ecology is concerned with the flow of energy in ecosystems. In effect, it is about applying the law of conservation of energy to ecological systems. You already know from Unit 22 that solar energy, trapped photo-synthetically by autotrophs, powers the entire living world. Light from the Sun falls on green plants—from giant trees to minute phytoplankton in oceans—and a very small fraction of that solar energy is trapped by their green tissues and used to fix carbon dioxide.

- ☐ Write down the simple equation that summarizes carbohydrate formation during photosynthesis.



Once formed (via the light and dark stages described in Unit 22), the carbohydrate serves first the plants themselves and then, through the various fates of the plants, heterotrophic organisms.

- ☐ Consider the growth of an acorn into an oak sapling. From what you learnt in Unit 22, identify the two main ways in which photo-synthetically produced carbohydrate serves the growing oak.
- ☒ The carbohydrate serves as building blocks and provides energy.

Carbohydrate formed in the chloroplasts is the precursor of almost all the organic material of the sapling (nitrogen, phosphorus and sulphur atoms being provided by ions absorbed through the roots). Equally important, carbohydrate is respired in cells throughout the plant. Oxygen is consumed by the mitochondria and ATP is produced, which then powers the range of energy-requiring reactions in the plant's cells. Ultimately, all the energy converted in respiration is dissipated as *heat*.

But what about heterotrophs—animals, fungi and most bacteria? These organisms cannot fix carbon dioxide by photosynthesis and depend, instead, on assimilating ready-made organic compounds from food. Within heterotrophs, the assimilated compounds fulfil the same two functions as they do in autotrophs. Some provide the organic building blocks that are used in the synthesis of new cellular compounds, and some are respired (usually by oxidation to carbon dioxide and water) with the associated production of ATP. The source of these organic 'food' compounds is, directly or indirectly, plants. Some examples are plain enough—zebras eat grass and lions eat zebras. But remember also that dead plants and animals decay. Think of the moulds and bacteria growing on a compost heap, or on the undigested plant material in a cow pat.

This is why we said earlier that carbohydrates produced by photosynthesis serve all heterotrophic organisms. In the following parts of this Section, we explore the routes along which energy flows from plants to other organisms in ecosystems. You will come across a number of technical terms that need to be learnt and, as always, you should be aware that data in Tables and Figures are often the results of many years of painstaking work in the field and laboratory. An important point to grasp, however, is that production ecology is dominated by the constraints of the *law of conservation of energy* (Unit 9). If x kilojoules of light energy falls on a square metre of grass in a given time, where does it go? Whatever its various fates, the parts must add up to the whole: the total *must* equal x .

2.1 PRIMARY PRODUCERS: GROSS AND NET PRIMARY PRODUCTION

If you consider any ecosystem—a lake, for example—it is plain that all organisms within it depend for their survival on an adequate supply of energy, and that their energetic needs will impinge on each other. In a lake, the fish, water-weeds, insects, birds, phytoplankton and zooplankton living in or on the water, are linked by their common need for energy. In this and most other ecosystems, solar energy enters the system via compounds produced in green plants. Not surprisingly, these photosynthetic autotrophs are described, in an ecological context, as **primary producers**.

Over the whole planet, primary producers make an astonishing quantity of carbohydrate each year—billions of tonnes, as you will see. But only a very small fraction of incident solar energy is converted into this stored chemical energy. The percentage conversion varies over the surface of the Earth, depending on vegetation present, but is frequently in the region of a mere 0.5–1.0%. Because life on our planet depends on energy given to us by our local star (the Sun), it is of interest to follow the fate of solar energy more closely.

You can see from Figure 2 that the Earth is bathed in light of remarkably constant intensity; we know this from meteorological experiments. In fact, just outside our atmosphere, each square metre perpendicular to the rays receives 1.4 kilojoules per second (1.4 kilowatts). This energy input is termed the solar energy flux and is roughly equivalent to the energy required to run between one and two bars of an electric fire. Much of this energy is lost long before it reaches the ground. Some is reflected back by clouds and dust, and some is absorbed by water vapour or dust, converted to heat and radiated back into space. Weather and latitude also affect both the quantity and monthly pattern of radiation reaching the ground at different places.

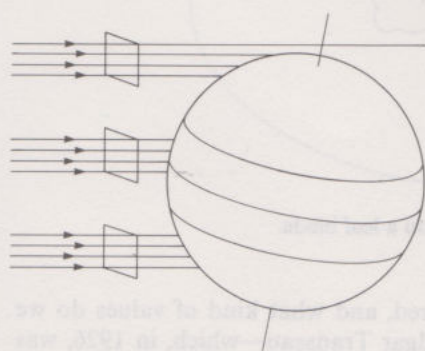


FIGURE 2 Solar energy flux. 1.4 kJ pass each second through each 1 m^2 window at right angles to solar radiation. The Earth is shown in its northern hemisphere winter position.

GROSS PRIMARY
PRODUCTION, *GPP*

PLANT RESPIRATION, *R*

NET PRIMARY
PRODUCTION, *NPP*

Of the solar energy that does reach ground, some falls not on plants but on soil, ice or rock. Of that falling on green cells, a small proportion is lost by reflection or passes straight through. Of the rest, about half lies in the ultra-violet and infrared regions of the electromagnetic spectrum (Unit 10) and is useless in photosynthesis. These 'useless' wavelengths—and most of the useful wavelengths too—are commonly used in evaporating water from leaf surfaces. This prevents leaves from overheating. Even with useful wavelengths, when the light energy is actually captured by chlorophyll molecules, some is still wasted in the biochemical inefficiencies of the light and dark reactions. In the end, only a small proportion of the incident light energy is converted into the *chemical energy of newly synthesized organic compounds*, and this captured energy is termed the **gross primary production (*GPP*)**.

GPP is usually expressed as the energy captured by plants on unit area of ground per unit time; the most commonly used units are $\text{kJ m}^{-2} \text{yr}^{-1}$. Whichever units are used, *GPP* represents the total energy captured photosynthetically by a quantity of plants in a given time. That capture, however, is only a temporary achievement as some of it is used by plants to power their own metabolism. The plants respire cellular chemicals by the routes you are now familiar with (Unit 22), and so make ATP. The rate at which organic compounds are used in this way is also measured in $\text{kJ m}^{-2} \text{yr}^{-1}$, and is termed **plant respiration (*R*)**. This energy is ultimately dissipated as heat and, if you think of respiration as a controlled burning process, it is easy to understand why. What is left, *GPP* minus *R*, is an expression of the net amount of organic compound accumulating in the plant (again in terms of $\text{kJ m}^{-2} \text{yr}^{-1}$). This unrespired portion of the original *GPP* is termed the **net primary production (*NPP*)**. We can now write the ecologically important equation

$$GPP = NPP + R$$

This relationship and the fate of solar energy falling on a plant are illustrated in Figure 3.

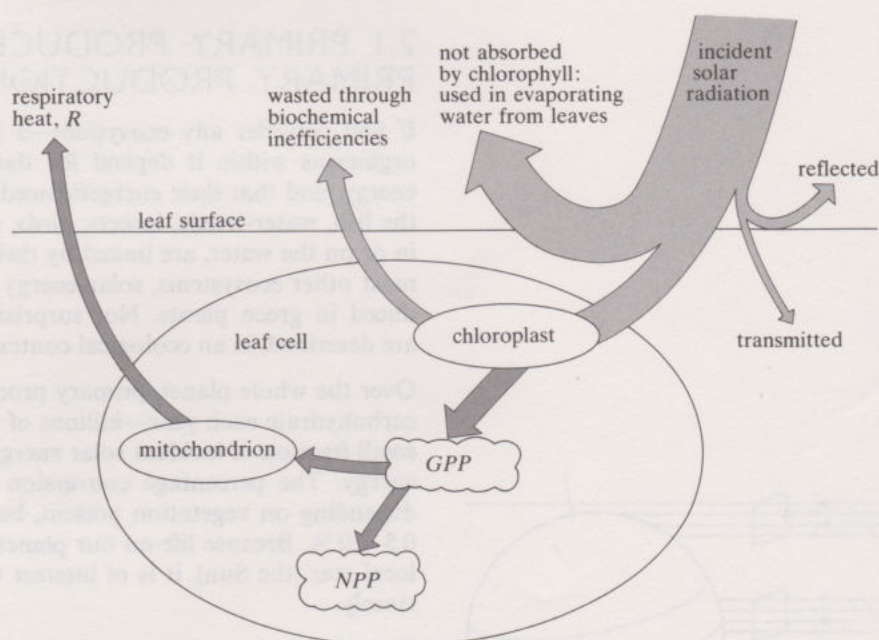


FIGURE 3 Fate of solar radiation falling on a leaf blade.

But how are *GPP*, *NPP* and *R* measured, and what kind of values do we find? A classic study in the USA by Edgar Transeau—which, in 1926, was way ahead of its time—illustrates, in essence, the approach. He estimated that his mid-western one-acre (4047 m^2) field contained 10 000 corn plants. By weighing several sample plants from the field, he next estimated that the total mass of the plants in the field was 6 000 kilograms. Then, using the

chemical analyses of other workers, he calculated that 6 000 kilograms of corn contained 2 675 kilograms of carbon. Next he argued that all this carbon was derived from photosynthetic glucose and that this was equivalent to 6 687 kilograms of glucose. (You can check this step yourself: $C_6H_{12}O_6$ is the formula of glucose, so $(6 \times 12)g$ of carbon are in $(6 \times 12) + (12 \times 1) + (6 \times 16)g$ of glucose, i.e. 180g of glucose contains 72g of carbon.) By other experiments (he measured carbon dioxide production at night), he estimated the additional glucose that the plants had already used in respiration and which he had, therefore, not been able to weigh. This value he put (for the whole field) at 2 045 kilograms of glucose. Burning one kilogram of glucose releases 15 790 kilojoules of energy as heat so, using this as a factor to convert from mass to stored energy, he was able to calculate the data shown in Table 1. He obtained the figure for incident solar radiation at ground level from other studies.

TABLE 1 Energy budget of one acre ($4047 m^2$) of corn, during one growing season of 100 days.

	Glucose/kg	Energy/ 10^6 kJ	% of incident solar energy
incident solar energy	–	8 580	100
<i>NPP</i> of maize	6 687	105.6	1.2
Respiration (<i>R</i>) of maize	2 045	32.3	0.4
<i>GPP</i> (<i>NPP</i> + <i>R</i>)	8 732	137.9	1.6

Corn does not grow all the year round, so production for the growing season is equivalent to annual production. We can, therefore, compare Transeau's data with more recent annual data given in Table 2 by making a simple area conversion. Since one acre is approximately equal to $4050 m^2$, his values for *NPP*, *R* and *GPP* are 26 000, 8 000 and $34\,000 kJ m^{-2} yr^{-1}$, respectively.

Although he used simple techniques, Transeau's values are quite similar to some of those in Table 2. The principle of this method and the underlying concepts are also as valid today as they were then. For *NPP* determination, modern methods depend on careful collection of all plant material produced in a given area in a given time, making allowances for any tissues that have been eaten or that have died and dropped off. This is followed by a determination of energy stored in the tissues, often using the technique of bomb calorimetry, which you met in TV 23.

TABLE 2 Average values for *NPP* in different ecosystems

Ecosystem	<i>NPP</i> / $kJ m^{-2} yr^{-1}$
extreme desert	260
desert scrub	2 600
subsistence agriculture	3 000
open ocean	4 700
areas over continental shelf	13 500
temperate grasslands	15 000
temperate deciduous forest	26 000
intensive agriculture	30 000
tropical forest	40 000

Since only net primary production is available for animals (including humans) to eat, *NPP* values are usually used to compare the 'productivity' of different ecosystems. Table 2 shows *NPP* values for some ecosystems. Note that they are *averages*, and the range within an ecosystem can be very large. Look at these values; can you think of reasons why they should be so different from each other?

You can probably identify some of the interrelated factors causing the variation in the figures in Table 2. They include density and type of vegetation, temperature (which affects particularly the length of the plant growing

BIOMASS
HERBIVORE
CONSUMPTION
FIRST CARNIVORE
HIGHER CARNIVORE
DETRITUS
DETRITIVORE
DECOMPOSER
FOOD CHAIN
TROPIC LEVEL

season), supply of soil nutrients and water, and the amount of light available in the growing season. Think also about the potential value of the open oceans as a major source of human food, bearing in mind that the primary producers are minute phytoplankton. Notice the low productivity of open oceans per unit area compared with intensively cultivated agricultural land, but remember that 70 % of the Earth's surface is covered by sea. In *theory*, human food requirements could be met by harvesting plants from this vast area, but in *practice* this is impossible: the phytoplankton are too thinly distributed and, even if we liked the taste, it would take too much energy to collect them. Another point of note from the Table is the difference in *NPP* between subsistence and intensive agriculture. This arises largely as a result of the application of nitrogenous fertilizers in intensive agriculture.

What happens to net primary production in a plant, i.e. to the chemical energy left over when the plant has respired some of the organic chemicals made by the leaves? The answer depends on the ecosystem you ask the question about and the time-scale being considered; but, as ITQ 1 shows, common sense may provide it.

ITQ 1 (a) Picture a saucer of cress seedlings on the kitchen windowsill. As they grow, what happens to the *NPP* up to the time that the cress is cut and eaten? What happens to the *NPP* after the cress is eaten? And what might happen to it if the whole saucerful died just before it was due to be harvested?

(b) Picture a small tropical island, densely packed with forest, uninhabited by humans and a great distance from any other land. Assuming that the total amount of plant and animal material remains constant from year to year, what happens to the *NPP* each year?

As you saw from the answer to ITQ 1 there are two routes for plant *NPP*. First, there is the part that remains inside the plant and manifests itself as growth, measurable as an increase in plant **biomass**; and second, there is the part that leaves the plant and enters the heterotrophic world. The biomass is the total dry mass, or the equivalent amount of energy (i.e. the energy that would be released if the mass were completely oxidized), of organisms in a given area, and is usually expressed as grams or kilojoules per square metre. The distribution of *NPP* between the two routes depends on both the age of the ecosystem and the types of plants in it. If the ecosystem contains mostly young, growing plants (like the saucer of cress or any young crop), then most *NPP* becomes new plant biomass. If the ecosystem is long established with a mixture of young and old plants (like the tropical island), and if you assume that its total biomass (i.e. the biomass of all plants, animals, fungi and bacteria) is *constant*, then all of the *NPP* passes to heterotrophs. The production of new plant or heterotroph biomass is balanced by the death and decay of old. Through whatever routes, the island *NPP* ends up being respired by heterotrophs, and so is ultimately converted to heat.

In the next Section we explore these routes further and look at the way in which *NPP* 'fuels' the heterotrophic world in general. First, however, let us consider the use that humans make of *NPP*. In common with other plant-eating heterotrophs, we take in and then assimilate some of the *NPP* (and ecology merges into agricultural science). In common with other animal-eating heterotrophs, we can also consume animals that have previously eaten plant material (and ecology merges into animal husbandry). However, other uses are unique to humans: plant *NPP* is directly harvested as wood, cotton, hemp, flax and rubber; it is indirectly harvested (via animals) in the production of wool, leather and guano (bird droppings used as fertilizer). We also make use of the *NPP* of plants that lived millions of years ago when we burn coal and oil, both of which are formed from dead plant material. Burning peat uses plants that died more recently. Other uses of the stored energy of *NPP* are being developed. Around two million cars in

Brazil are powered almost entirely by ethanol (ethyl alcohol) made by fermenting the juice of sugar cane. The intention, of course, is to replace expensive, imported and irreplaceable fossil fuels by the constant supply of alcohol from home-grown sugar cane.

2.2 FOOD CHAINS AND FOOD WEBS: HETEROTROPHIC NUTRITION

In principle, the story of energy flow from plants to heterotrophs is simple and, at the cartoon level, Figure 4 makes the point. While some *NPP* may remain stored within plants and increase plant biomass, some may be grazed by plant-eating animals—the **herbivores**. The energy input to herbivores is called **herbivore consumption**. In a pasture, about 40 % of annual grass production may be consumed by cows, but in a forest only about 2 % of *NPP* usually passes to grazers. The herbivores may themselves be preyed upon by other animals, the **first carnivores**, and these may be eaten by still other animals, the **higher carnivores**. The energy input to these animals is termed **carnivore consumption**. Returning to plants, a final part of the *NPP*—contained in dead leaves, plants, flowers and so on—reaches the ground, where it provides food for a variety of heterotrophs. Some of these are small animals, such as nematodes or earthworms, that feed on this dead organic matter, which is called **detritus** or **litter**; these animals are called **detritivores**. Others are the fungi and bacteria of the soil and are collectively called **decomposers**. These soil micro-organisms are the ultimate consumers of all dead organic material in ecosystems and, because they live in or on detritus, they too are eaten by detritivores.

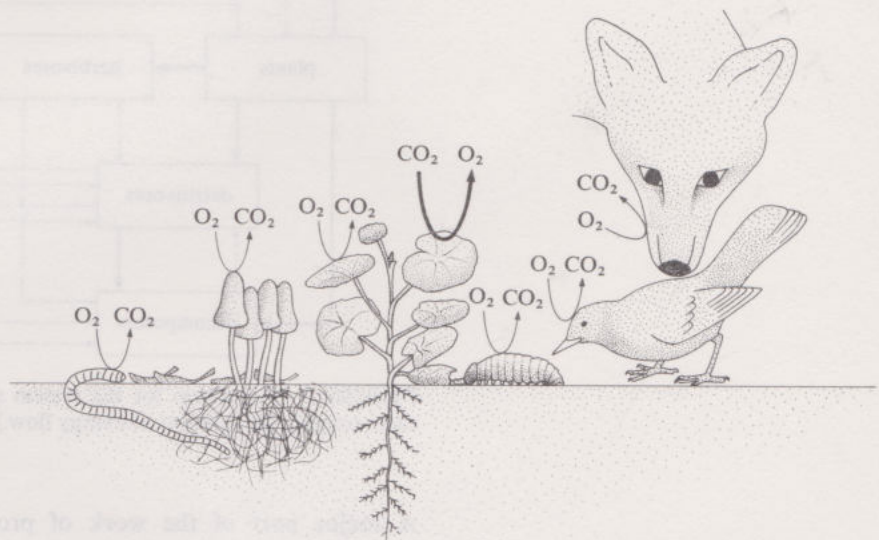


FIGURE 4 Heterotrophs depend on plants: food chains.

- ☐ Using standard terminology, what will be the name used to describe energy inputs to detritivores and decomposers?
- ☒ Detritivore consumption and decomposer consumption respectively.

If you look at Figure 4, you will see a number of linear sequences of 'organisms eating organisms eating plants'. The most obvious is

plant → caterpillar → bird → fox

and is an example of a **food chain**. Each organism occupies a particular feeding level or **trophic level** (*troph* is from the Greek for food, as you may remember from the discussion of *autotroph* and *heterotroph* in Unit 22). The plant-to-fox chain has four trophic levels, and it can be rewritten in more general terms:

plant → herbivore → first carnivore → higher carnivore

FOOD WEB

ASSIMILATION

There is, of course, an enormous number of food chains across the large range of habitats on the planet. However, it is rare to find chains of more than about five trophic levels—sharks are not eaten by super-sharks. Marine food chains that start with ultra-small phytoplankton may have ten or more links, but the factors that determine the length of food chains are still a puzzle to ecologists. Moreover, the food relationships in an ecosystem are usually more complicated than those of a simple chain.

- Look again at Figure 4 and imagine some of the food relationships that have been omitted in this simple drawing. Can you see other food chains or relationships between food chains?
- Plant leaves, when rotten and covered with bacteria and fungi, are eaten by earthworms—and these, in turn, die and are consumed by decomposers. Worms as well as caterpillars are the prey of birds and foxes. And, as many irate farmers confirm, foxes will eat tender crops and fruit as well as chickens. Birds may also eat plant material as well as animals; and all animals die and supply the detritivores and decomposers with more material for consumption.

So, there are in the cartoon *several* food chains, and a given organism may feed at *more than one* trophic level. This complex set of relationships is described as a **food web**. Figure 5 shows a food web (still simpler than reality), based on Figure 4 but presented in a generalized form.

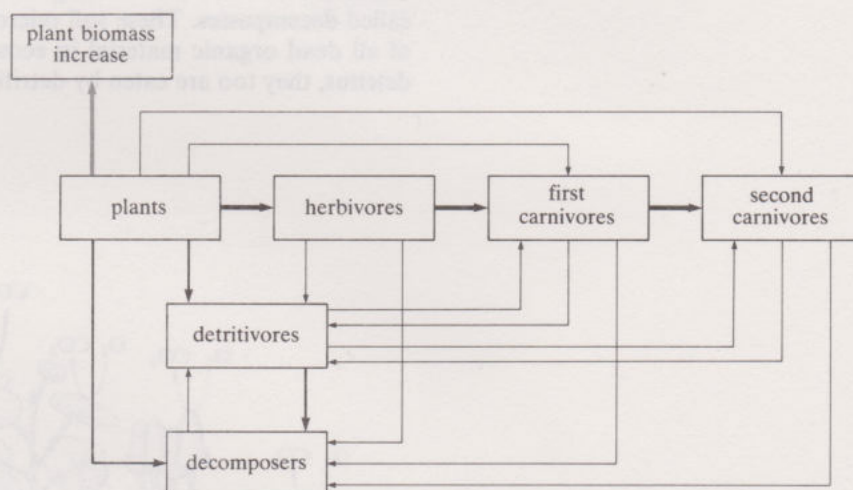


FIGURE 5 Food web for the system shown in Figure 4. (Thickness of line indicates roughly the amount of energy flow.)

A major part of the work of production ecologists has been directed towards working out the details of particular food webs, and then establishing the paths and quantities of energy flowing through them. Constructing a web involves protracted field work combined with laboratory studies. The main approaches include observation of the predator/prey relationships; laboratory food-preference experiments (to give only indications of what may or may not be likely in the wild); analyses of gut contents, regurgitated food pellets and faeces; and isotopic labelling studies. In the latter, plants are labelled with an unstable isotope, such as ^{32}P , and nearby animals are captured and checked at regular intervals. All the animals that feed on the plants, directly or indirectly, become labelled; herbivores reach their peak radioactivity quickly, while top carnivores incorporate isotope much more slowly.

Once the routes within a food web have been established, an attempt can be made to quantify the flow of energy through the web. To do this, attention

must be paid not only to the energy *entering* a trophic level (*GPP* or consumption), but also to how much of this energy is stored (resulting in biomass change) and how much is 'lost' (in respiration, through death, or in faeces and urine, for example).

- Imagine sheep eating grass on a hillside. Sheep's droppings are much in evidence. Clearly only part of the herbivore consumption is entering the bloodstreams of the sheep after digestion. This fraction is called herbivore **assimilation**. The balance is represented by the energy content of the faeces. In what way are these three quantities related arithmetically?
- Herbivore consumption = herbivore assimilation + faecal energy content.

Though the energy route may be very complicated, the methods that are used to trace the flow of energy are simple in principle. Energy flow calculations depend on the following four procedures.

1 The flow of mass of organic material must be monitored by careful field sampling and measurements. What dry mass of plant material enters the herbivore/carnivore food chains and the detritivore/decomposer food chains? Is there, over the period of study, any net increase in plant biomass? What mass is consumed at each trophic level? What proportion of this is lost in faeces or in other ways (urine, hair etc.), and are there changes in net annual biomass over the period?

2 The organic masses measured in (1) must be converted to energy (kilojoule) equivalents. This can be done using bomb calorimetry techniques of the type you saw in TV 23.

3 For animals, respiration, in kilojoules must be found. This can be determined, theoretically, by subtraction (consumption, minus energy loss in faeces etc., minus biomass increase or production). However, it is more commonly found by direct measurement of the amount of oxygen used or carbon dioxide produced. Remember from Unit 22 that six moles of O_2 are used (and six moles of CO_2 are produced) in the production of 2800 kilojoules of energy when glucose is the fuel. Slightly more complex calculations are necessary for 'mixed fuel' oxidations (i.e. of fat and protein as well as carbohydrate) as different chemical equations and heat outputs are involved.

4 For plants, respiration and *GPP* must be found. This is more complicated because photosynthesis (CO_2 uptake and O_2 production) and respiration (CO_2 production and O_2 uptake) occur together in the light. However, experiments in which gas changes are measured in both light and dark provide the necessary information. Another approach in determining *GPP* is to surround leaves, in a closed vessel, with $^{14}CO_2$ and measure the rate at which it is incorporated into the illuminated plant over a short period of time.

With careful measurements along these lines, it is possible to construct an energy flow diagram for a particular ecosystem. In Section 2.3 we shall consider a real example: energy flow in a river ecosystem. Before that, however, we shall try out some of the ideas involved, using a simplified system based on Figure 5 and the organisms in Figure 4.

Suppose that careful measurements over one year show that (a) the biomass of woody plants in the ecosystem increases by a modest amount equivalent to E_1 kJ, (b) an amount of plant material equivalent to E_2 kJ dies and enters the detritivore/decomposer chain (i.e. is eaten by worms and colonized by fungi and bacteria), and (c) plant material equivalent to E_3 kJ enters the grazing food chain (i.e. is eaten by the caterpillars). This is shown in Figure 6 (overleaf). Note that $NPP = E_1 + E_2 + E_3$ (but if, by the way, there had been no biomass increase, it would have been the case that $NPP = E_2 + E_3$).

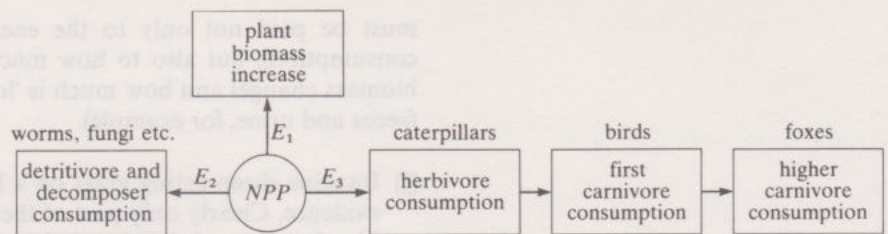


FIGURE 6 Net primary production (NPP) may increase plant biomass (in this case E_1), may be consumed by detritivores and decomposers (E_2) or may be consumed by herbivores (E_3). The relationship $NPP = E_1 + E_2 + E_3$ applies.

This is just the first stage of analysis. Herbivore consumption, E_3 , is in this case caterpillar consumption, so we can call it E_{cC} as in Figure 7.

- ☐ Is E_2 equivalent to detritivore/decomposer consumption?
- ☒ No: you can see from the bottom line in Figure 7 that there is another input to these organisms, which is discussed below. Dead plant material is the major but not the only food available to soil heterotrophs.

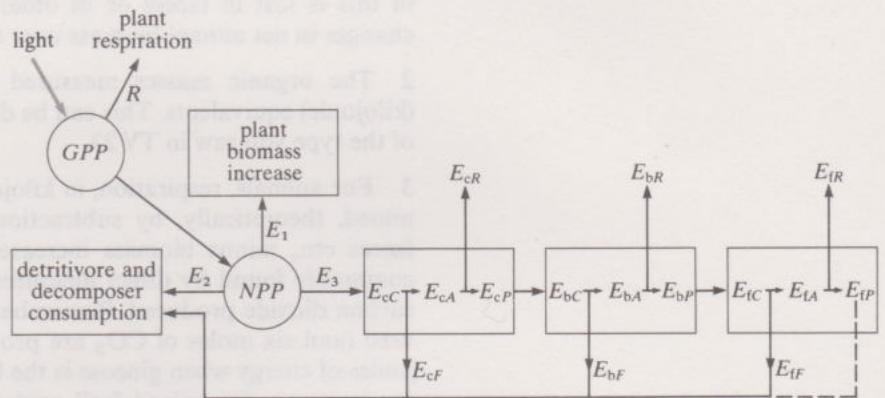


FIGURE 7 The flow of energy through trophic levels of the simple food chain plants → foxes. Ignore the dotted line until this is mentioned in the text. Note that $E_3 = E_{cC}$.

Now, using Figure 7, let us follow through what happens to caterpillar consumption. Some of it remains undigested and is eliminated as caterpillar faeces (E_{cF}). The rest is absorbed from the gut and assimilated (caterpillar assimilation, E_{cA}).

- ☐ How are E_{cC} (or E_3), E_{cA} and E_{cF} related?
 - ☒ E_{cC} (or E_3) = $E_{cA} + E_{cF}$
- Some of E_{cA} is respired (caterpillar respiration, E_{cR}), and some of it is left in the form of new cell material (caterpillar production, E_{cP}).
- ☐ How are E_{cA} , E_{cR} and E_{cP} related?
 - ☒ $E_{cA} = E_{cR} + E_{cP}$. (This is analogous to the relationship between GPP , R and NPP in plants.)

Some caterpillars are eaten by first carnivores (birds, b) which, in turn are preyed on by higher carnivores (foxes, f). At each of these trophic levels the sequence of consumption, faecal production/assimilation, respiration/production is repeated, and you can follow this through in Figure 7. Generally, only about 10 % of the energy entering (consumed by) one trophic level is consumed by the next trophic level. Note that all faecal material (E_{cF} , E_{bF} , and E_{fF}) passes to the detritivores/decomposers, so this is one of the additional inputs to these organisms that we mentioned above.

Now, since the convention adopted in Figure 7 is that all energy flows through the boxes and is ultimately either dissipated as heat in respiration

or, in the case of plants, stored as new biomass (E_1), this Figure has certain implications about the flow of energy along the grazing chain, from caterpillars to foxes.

- ☐ What is implied about the biomass of these three types of consumer?
- That it is constant from year to year: none of the production (E_{cP} , E_{bP} or E_{fP}) is stored.

This is perfectly reasonable if we assume that the animal populations are stable, and it is the logic behind the dashed line in the Figure: fox production must be accounted for somehow. What this dashed line implies is that during one year an amount of energy equivalent to E_{fP} passes to the detritivores/decomposers as dead foxes. However, Figure 7 also implies that *all* caterpillar production is consumed by birds and that *all* bird production is consumed by foxes (i.e. $E_{cP} = E_{bC}$ and $E_{bP} = E_{fC}$). This is highly improbable and numerous studies have shown that the amount consumed by one trophic level rarely exceeds 25 % of the production of the preceding trophic level. So to make Figure 7 more realistic you should draw in dashed lines from E_{cP} and E_{bP} to join the bottom line leading to detritivores/decomposers: dead caterpillars (or moths if they develop fully) and dead birds balance the energy budgets at these trophic levels.

Figure 7 is still not a full representation of Figure 5. The consumption of detritivores by carnivores (birds and foxes eating the worms) has not been included, for example. However, it does illustrate how the energy entering a very simplified ecosystem can be accounted for: *all the light energy trapped by plants in this system during photosynthesis (GPP) is ultimately dissipated as heat during respiration or stored as plant biomass, E_1 .* The validity of this statement rests on two critical assumptions about the biomass of heterotrophic consumers and the activity of decomposers.

- ☐ Recall the first assumption and try to guess the second.
- (a) The biomass of heterotrophic consumers is constant (averaging from year to year). (b) The decomposers (bacteria and fungi), which are the ultimate consumers of dead organic matter, break down *all* that they receive during the year, i.e. there is no accumulation of dead organic matter in the soil.

Assumption (a) is true for ecosystems at steady state (i.e. where total energy input equals total energy output, as in the tropical island in ITQ 1), and in the *short* term for most ecosystems. In the *long* term, however, there are many ecosystems for which it is false. This is often a result of human interference or simply human presence: the biomass of humans, for example, has increased by a factor of about 1 500 over the last 10 000 years.

Assumption (b) is also not true for all ecosystems. In a peat bog, for example, the cold, wet, acidic conditions slow down decomposition so that about 10 % of the dead material entering the detritivore/decomposer food chain in any year is not broken down. This builds up slowly as peat.

Before looking in detail at a real food web, it is helpful to summarize the main things that characterize webs in general. First, energy usually enters a food web from one source, the Sun. You will see in Section 2.3, however, that energy inputs in the form of organic matter may also occur and in some special cases (such as cave ecosystems, where there is no light) all energy enters in this way. Second, energy *flows through* a food web, from one trophic level to another. Third, a food web is 'leaky': only about 10 % or less of the energy entering one trophic level is passed on to the next. This is not to say that the law of conservation of energy is violated, but simply that some of the energy taken in is not assimilated and much of what is assimilated is then dissipated as heat during respiration: only the small part left is available to organisms in the next trophic level. Fourth, food webs rarely contain more than five trophic levels. Finally, when the total biomass in an ecosystem is constant over a given period, the total energy intake from the Sun (GPP) plus the energy of any inputs of organic matter equals the total respiratory energy dissipated as heat across all trophic levels. This is the inevitable consequence of energy conservation.

2.3 ENERGY FLOW IN AN AQUATIC ECOSYSTEM

Producing an energy budget for even the simplest natural ecosystem could be a mammoth task as it could involve measurements of the food consumption, respiration, growth and reproduction of a very large number of organisms. In practice, estimates of energy intake and use are made for the organisms that appear to be most 'important', that is to have the highest biomass or the highest production at each trophic level; the uncertainties are often high because of the variability of the populations and the difficulties in sampling them. What follows is a description of the energy flow in an aquatic ecosystem. The details are not important and you need not remember them. The aim is to illustrate the ideas introduced earlier.

The results of an investigation of part of the River Thames are summarized in Figure 8. Work on this ecosystem involved nearly 20 biologists over a period of more than seven years, but even so they were not able to quantify all the links in the food web. In Figure 8 the situation has been simplified and some energy values from other research have been included to give you a fuller picture. Look first at the organisms, ignoring the numbers for the moment. The principal primary producers are small plants called diatoms, which are suspended in the water and multiply rapidly if conditions are suitable. These form part of the phytoplankton, and are eaten by the small swimming animals of the zooplankton. The water fleas or *Daphnia* that you saw in TV 22 are examples of zooplankton.

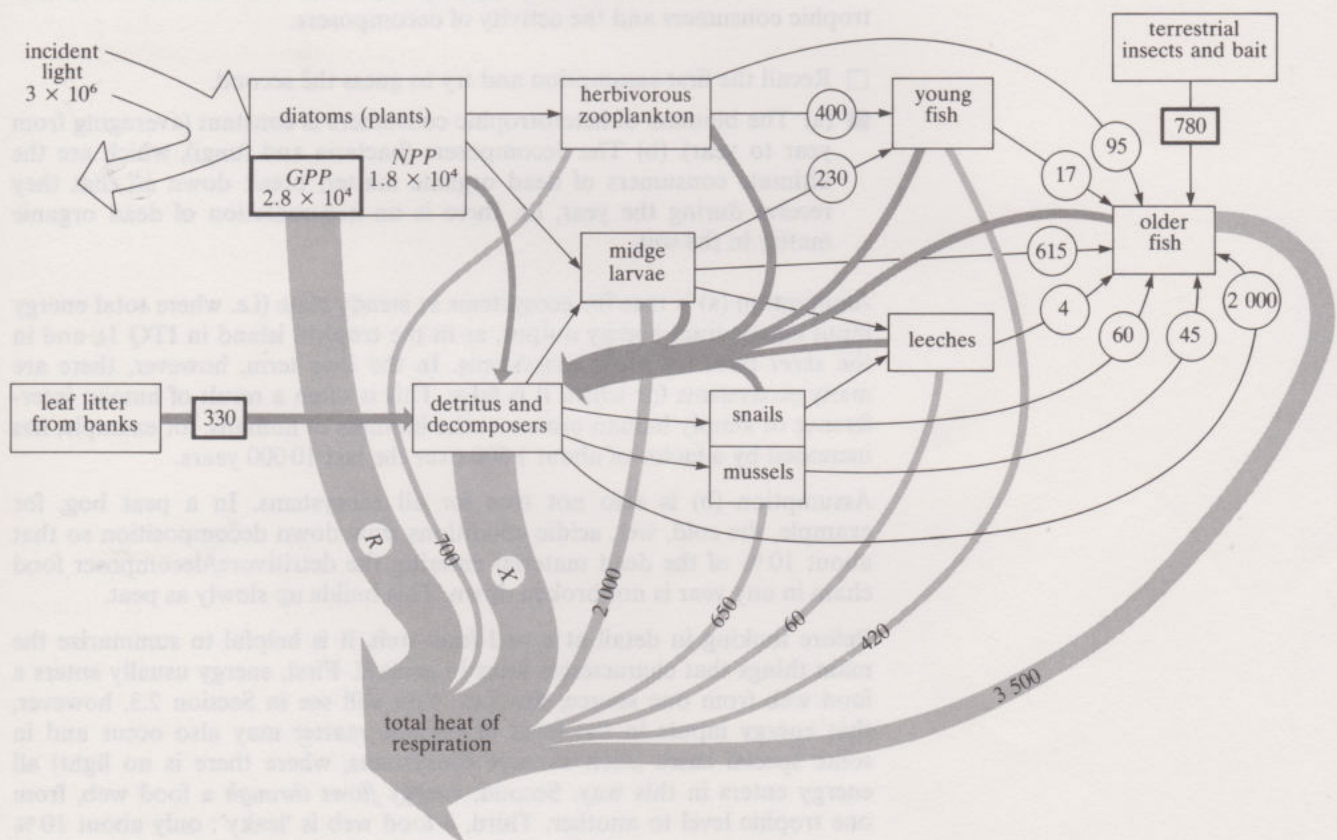


FIGURE 8 A simplified energy flow diagram for part of the River Thames. Read the text for explanations of the arrows and numbers. All values are given in kJ m² yr⁻¹.

The young fish are bleak, *Alburnus*, and roach, *Rutilus* (Plate 4), that are less than one year old. The midge larvae belong to an insect group called chironomids and are very common in the silty bottoms of rivers and lakes. Water snails and freshwater mussels are molluscs; the former move over the bottom, feeding by grazing, and the latter live partly buried in mud and draw a stream of water through their bodies, extracting small particles from it. The leeches move actively over the bottom and devour midge larvae and snails.

Now consider the energy flow in this ecosystem. Thin black arrows indicate food links in all parts of the food web except those connected with the decomposer/detritivore chain. The figures in circles show the amount of food consumed in each link. The dark grey arrows show the transfer of dead organic matter from various sources to the decomposers and to the detritus pool (these two cannot be separated here); most numerical values have been omitted for clarity. As regards energy *inputs* to the ecosystem, the values of three are shown in the boxes with heavy black edges. Notice that only a tiny proportion (0.9 %) of the energy from sunlight falling on the water is 'fixed' by diatom photosynthesis into gross primary production, and only 0.6 % of this incident energy becomes available as net primary production. A second, much smaller, input is as dead leaves etc. ('litter') from the adjacent river bank ecosystem. In addition, this part of the Thames is heavily fished by anglers (who return their catch to the river), and the older fish have a food input in the form of bait (bread and maggots) and terrestrial insects that fall onto the surface of the water. The only energy *output* is the heat dissipated through respiration, and values for this are shown on the thick, pale grey arrows. Now use the information in Figure 8 to answer ITQs 2 to 5.

ITQ 2 What is the total energy input to this ecosystem and what proportion of the total derives from photosynthesis by plants in the system?

ITQ 3 Calculate the value of *R*, the respiration of plants.

ITQ 4 Assume that the total biomass of the ecosystem is constant when averaged from year to year and that there is no net accumulation of detritus on the river bed. Using the information in Figure 8 and the values for total energy input and *R* calculated above, how would you calculate the value of *X* (the respiration of decomposers living on detritus) in Figure 8? Do the calculation if you have time.

ITQ 5 To what trophic levels do the following belong? (a) midge larvae; (b) young fish; (c) leeches; (d) older fish; (e) snails.

As you can see from Figure 8 and the answers to these ITQs, this River Thames ecosystem differs in various ways from the self-contained model ecosystem of Figures 5 and 7. It has inputs of energy from other ecosystems (the bank and the area from which the anglers' bait and the insects come), and some of the groups of organisms (notably the older fish) straddle several trophic levels. But this is a real ecosystem, and the study of energy flow through it emphasizes three important facts. First, *dead* plant material, in the form of detritus, may be a very important food source for animals, sometimes more important than living plants. Second, *decomposers* (bacteria and fungi) may dissipate large amounts of energy (in this case, $1.2 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$ out of a total of $2.9 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$, i.e. over 40 %). This shows the importance, which is often overlooked, of decomposition in ecosystems. Third, finding whether there is an energy balance depends on a knowledge of any overall biomass changes.

SUMMARY OF SECTION 2

1 Solar energy is trapped by photosynthesis in plants. This energy is called the *gross primary production (GPP)*, and it fuels not only the plants but also the entire heterotrophic world. As plants have this primary role, they are called *primary producers*. Only about 0.5–1.0 % of incident solar energy is captured as *GPP*.

2 The part of the *GPP* that is oxidized by plants is termed *plant respiration (R)*. The part that is left is called the *net primary production (NPP)*.

$$GPP = NPP + R$$

The most common units for the quantities in this equation are $\text{kJ m}^{-2} \text{yr}^{-1}$.

3 Different ecosystems have different productivities (that is, annual *NPP* values). Tropical forests usually have one of the highest productivities and deserts have the lowest.

4 The biomass of all plants in a given area is the total dry mass of plant material, or the amount of energy in kilojoules potentially available through oxidation of this mass. Part of the plant *NPP* may be stored as new plant biomass, while the balance enters heterotrophic food chains as either living or dead material (litter or detritus). If plant biomass in an ecosystem is constant, then all *NPP* must be entering heterotrophic food chains.

$$NPP = \text{plant biomass change} + \text{herbivore consumption} + \text{dead material passing to detritivores/decomposers}$$

5 Humans make direct use of *NPP* (as plant-eaters and through other kinds of plant cropping) and indirect use of *NPP* (as flesh-eaters and through other kinds of animal cropping).

6 The level at which an organism feeds is called its *trophic level*. The flow of energy between trophic levels can be represented as a *food chain*. These interlink to form food webs. The terms used to describe the trophic levels of heterotrophs are *herbivore*, *first* or *higher carnivore*, *detritivore* and *decomposer*.

7 For animal consumers, the following relationships are important in calculating energy flow through food webs:

$$\text{consumption} = \text{assimilation} + \text{faecal production}$$

$$\text{assimilation} = \text{production} + \text{respiration}$$

8 A range of experimental methods is involved in *establishing* the links in a food web and in *measuring* energy flow along the links.

9 Energy *flows through* an ecosystem but it may be stored as chemical energy for varying periods in biomass or in dead organic matter in the soil or sediments. If both of these are constant when averaged over a year or more, then the ecosystem is in a steady state and total energy inputs must equal total energy outputs. If there is no export of material from the system (e.g. by harvesting or migration of animals) then the sum of energy inputs equals the sum of respiratory energy outputs, i.e. all energy entering the ecosystem is dissipated as heat. This equivalence is also an inevitable outcome of the law of conservation of energy.

10 Generally, only about one tenth of the energy consumed by organisms of one trophic level is available for consumption by organisms of the next trophic level. This is a consequence of respiration, faecal output, and loss, through death, to detritivores and decomposers.

SAQ 2 Is each of the following statements true or false? Give reasons for your answers.

- Carnivores are autotrophs.
- Consumers and decomposers are heterotrophs.
- Green plants are primary producers; they 'fix' some of the energy in sunlight by the process of photosynthesis.
- Energy flows through a community and is then recycled, i.e. it flows through again.
- All detritivores are omnivorous heterotrophs.
- The increase in biomass of a population over one year always equals the annual production of that population.
- All the net primary production of an ecosystem is immediately consumed as food by herbivores.

SAQ 3 The following relationships may be observed on a rocky British shore, some when the tide is in, others when the tide is out:

- limpets grazing on diatoms attached to the rocks;
 - dogwhelks eating barnacles and mussels;
 - crabs consuming detritus and dead mussels in crannies in the rocks;
 - barnacles feeding on zooplankton;
 - mussels feeding on phytoplankton diatoms;
 - flat periwinkles feeding on diatoms attached to seaweeds;
 - gulls feeding on dead crabs;
 - turnstones (birds) feeding on dogwhelks, limpets and periwinkles.
- Which of the feeding organisms in (i) to (viii) are: herbivores; first carnivores; higher carnivores; detritivores; decomposers?
 - Construct one complete food chain from the list (this need not include all the listed species). Would it be possible to construct any other food chains? Is this ecosystem better described as a series of food chains or as a food web?

SAQ 4 Table 3 gives values (in $\text{kJ m}^{-2} \text{yr}^{-1}$), based on two of three measurements, for food assimilated (*A*), respiration (*R*) and production (*P*) by populations of animals U to Z. Calculate the missing values (a) to (f).

TABLE 3 Production ecology data. All values are given in $\text{kJ m}^{-2} \text{yr}^{-1}$. For use with SAQ 4.

Animal population	<i>A</i>	<i>R</i>	<i>P</i>
U	(a)	68	2
V	104	78	(b)
W	14	(c)	0.2
X	(d)	14.8	0.5
Y	638	590	(e)
Z	638	(f)	12

BIOGEOCHEMICAL CYCLES

SAQ 5 In a large freshwater stream in the USA, the values shown in Table 4 were measured, all in $\text{kJ m}^{-2} \text{yr}^{-1}$.

(a) Calculate the missing value, x .

(b) Figure 9 is a food web for the freshwater stream and the boxes V to Z represent the trophic levels involved. By reference to Table 4, identify each box.

(c) By comparing overall respiration with *GPP*, decide whether this is a self-contained ecosystem as far as energy is concerned, or whether there is a net import or a net export of energy. Again, assume that total biomass is constant and also that the total amount of detritus remains constant.

TABLE 4 Freshwater stream data. All values are given in $\text{kJ m}^{-2} \text{yr}^{-1}$. For use with SAQ 5.

	Gross primary production	Respiration	Net primary production
plants	9.0×10^4	5.0×10^4	x
	Food assimilated	Respiration	Production
herbivores	12.0×10^3	10.3×10^3	1.7×10^3
first carnivores	1.5×10^3	1.3×10^3	0.2×10^3
higher carnivores	10.0×10^1	6.0×10^1	4.0×10^1
decomposers	2.0×10^4	1.8×10^4	0.2×10^4

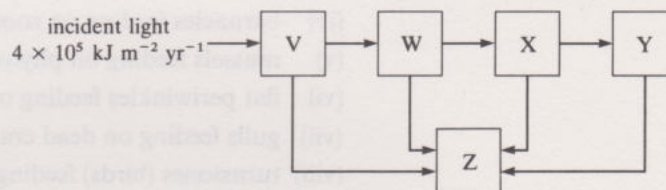


FIGURE 9 Food web for a freshwater stream.

3 CARBON, NITROGEN AND MINERAL CYCLES

A continuous supply of energy is *one* of the essential requirements for life and, as you saw in Section 2, sunlight is the ultimate fuel for living organisms on this planet. But organisms are made of chemicals—water, ions and organic molecules of many kinds—and a supply of these substances (or the raw materials to make them in cells) is also a requirement for life. Table 5 shows the range of elements necessary for life, and the number is quite large.

For organisms on Earth, however, there is a crucial difference between the supply of energy and that of chemical raw materials: energy is available in ample supply from outside Earth (from the Sun) but there is no extra-terrestrial supply of materials. We have a fixed amount of materials available on Earth—and that is all. Consequently, the chemicals needed to build bodies are used and then re-used, over and over again. They move in a *cycle* from the soil, water or atmosphere into plants and animals and back again. A molecule of oxygen that you breathe in now may have been released by an oak tree (during photosynthesis) a few hundred years ago.

TABLE 5 Elements necessary for life, and some of their functions.

Category	Element	Symbol	Some known functions
Major constituents (20–60 % of atoms)	hydrogen	H	Universal components of organic compounds in cells
	carbon	C	
	oxygen	O	
macronutrients (0.02–2.00 % of atoms)	nitrogen	N	Essential constituents of proteins and amino acids
	sodium	Na	Important ion involved in generation of nerve impulses
	magnesium	Mg	Activator of many enzymes*; also a constituent of chlorophyll
	phosphorus	P	Universally involved in energy-transfer reactions and in nucleic acids
	sulphur	S	Found in proteins and other important substances
	chlorine	Cl	One of the major anions in cells
	potassium	K	Important cation involved in nerve conduction, muscle contraction, etc.
	calcium	Ca	Important constituent of cell membranes and regulator of cell activity
micronutrients (‘trace elements’; less than 0.001% of atoms)	boron	B	Important in plants, probably as co-factor of enzymes
	silicon	Si	Found abundantly in cell walls of grasses and many algae such as diatoms
	manganese	Mn	Activator of many enzymes*
	iron	Fe	Activator of many oxidative enzymes*; also in haemoglobin
	cobalt	Co	Constituent of vitamin B ₁₂ , required for N-fixation
	copper	Cu	Activator of many oxidative enzymes*
	zinc	Zn	Activator of many enzymes*; also insulin
	molybdenum	Mo	Activator of a few enzymes*, particularly nitrogenase (used in N-fixation)
	iodine	I	Constituent of thyroid hormones, which affect growth and development in vertebrates

* Metal activators bind to enzymes and are necessary for catalytic action.

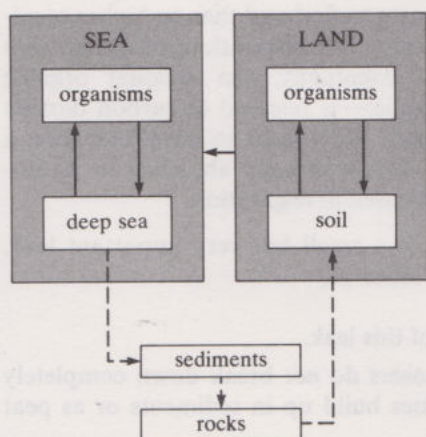


FIGURE 10 Generalized biogeochemical cycle of a mineral nutrient. Dashed lines indicate very small transfers.

Cycles that operate on a grand scale between rocks, soil or sea, organisms and air are called **biogeochemical cycles**. The carbon cycle (Section 3.1) is an example, and the oxygen and water cycles are also of this scale. A major part of these cycles involves movement of molecules into and out of the air (as carbon dioxide, oxygen and water vapour, respectively), and since air is a global reservoir they can only be studied globally. However, the biogeochemical cycles of other elements, with the exception of nitrogen (Section 3.2) and sulphur, do not involve the atmosphere. Figure 10 is a generalized version of this type of cycle; note three things about it:

- 1 There are two sub-cycles: one in the sea (between organisms and the deep sea) and one on land (between organisms and soil).
- 2 These sub-cycles are ‘leaky’: the land cycle leaks into the seas as dissolved ions and eroded soil are washed out via rivers, and the marine cycle leaks as sediments are deposited on the sea-bed and eventually form sedimentary rocks.
- 3 The leaks are plugged and the biogeochemical cycle completed by the breakdown of rocks (a process called weathering). Rock formation and weathering are very slow processes and what matters for ecosystems on land is whether *local* leaks, in particular ecosystems, are compensated for.

MINERAL CYCLE

CARBON CYCLE

So the cycles of these elements, which do not involve gases, are usually studied locally within an ecosystem, not globally. These local cycles are called **mineral cycles** because the main reservoir of the elements is as minerals in rocks. We shall consider them briefly in Section 3.3.

3.1 THE CARBON CYCLE

Having studied Unit 22 and Section 2 in this Unit, you already know quite a lot about the 'bio' part of the biogeochemical **cycle of carbon**.

- ☐ Draw a simple carbon cycle involving only organisms and the atmosphere. Recall which gases are taken up and released during photosynthesis and respiration. Bear in mind that organic molecules, by definition, contain carbon; they are also a form of 'stored' chemical energy, so carbon and energy move together as organic matter.
- Anything that resembles Figure 11 will do.

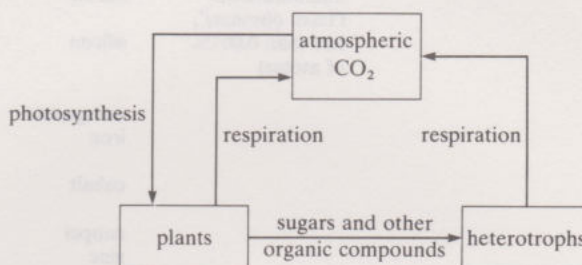


FIGURE 11 The biological part of the carbon cycle on land.

The essential features are that plants (autotrophs) take up carbon as carbon dioxide from the air (or, if they are aquatic, from solution in water) during photosynthesis. The carbon dioxide is reduced to a simple organic molecule—glucose—which may then be converted to any of a whole range of other organic compounds. Some of these compounds are oxidized by plants during respiration, which provides metabolically useful energy (in the form of ATP) that is eventually dissipated as heat, and releases *carbon dioxide back into the atmosphere*. Other organic compounds may be stored as plant biomass but, ultimately, either when the plant dies or is eaten by a herbivore, organic carbon passes to heterotrophs. Heterotrophs cannot use carbon dioxide as a source of carbon. Carbon in organic molecules may undergo several transfers between heterotrophs on different trophic levels (as you saw in Section 2)—from herbivores to first and then to higher carnivores, for example. All these animals carry out respiration, releasing *more carbon dioxide into the atmosphere*. Eventually, the residual organic carbon—i.e. that in faeces and dead bodies—is released as carbon dioxide through the activities of the decomposers. We appear to have, therefore, a perfect biological cycle in which the carbon dioxide absorbed in photosynthesis balances the carbon dioxide released in respiration.

In fact the cycle is not perfect. There is a small but very important leak, without which we would have no coal, oil or peat.

- ☐ Recall from Section 2.1 the nature of this leak.
- In certain ecosystems, the decomposers do *not* break down completely all dead organic matter. The residues build up in sediments or as peat

and provide a store of energy and carbon. This store, accumulated over millions of years, is our fossil fuel reserve.

Apart from this very small leak, the amount of carbon taken up in photosynthesis does equal the amount released in respiration. The eruption of volcanoes and the weathering of rocks rich in calcium carbonate (limestone and chalk) releases small extra amounts of carbon dioxide into the atmosphere, but this is roughly balanced by the deposition of carbonate in sediments. There is also a huge buffering system, provided by the oceans, which are in equilibrium with the atmosphere: carbon dioxide dissolves in water forming bicarbonate and carbonate ions, or is released into the atmosphere, to maintain equilibrium. (This involves the same reversible reactions you met when carbon dioxide dissolves in blood.) So the carbon cycle *should* be in dynamic equilibrium: the amount of carbon in different compartments—living organisms, the atmosphere, the oceans and the land (soil and rocks)—should be roughly constant, with fluxes of carbon into any compartment balanced by fluxes out. This balanced state is shown in Figure 12.

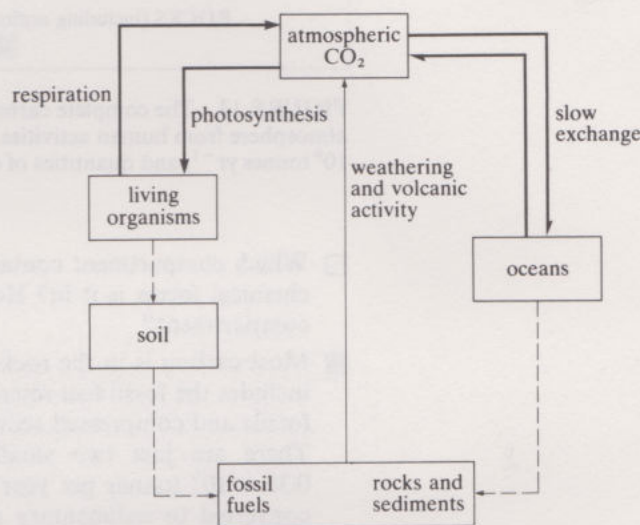


FIGURE 12 The carbon cycle in a balanced state. The oceans act as a buffer to maintain a constant level of carbon dioxide in the atmosphere. Dashed lines indicate very small transfers.

However, two kinds of human activity have begun to alter the balance of the carbon cycle. The first of these is the burning of fossil fuels (coal, oil and gas), which releases into the air annually about 5 % as much carbon dioxide as the respiration of all organisms. The second, which it has been estimated releases up to twice as much carbon dioxide as fossil fuel burning, is the clearing of forests coupled with ploughing. This may seem surprising, but at present over six million hectares (i.e. $6 \times 10^{10} \text{ m}^2$) of tropical forest are being cleared each year. This yields large amounts of carbon dioxide, partly when the wood is burnt and partly when the cleared land is ploughed and aerated, which oxidizes and accelerates the decomposition of organic matter in the soil.

If we put together the biological and the geochemical parts of the carbon cycle and quantify them, you will see these human effects in perspective. How much carbon is there on Earth, where is it and in what forms is it? The quantified cycle is shown in Figure 13, although many of the values are crude estimates. Look at this Figure and then answer the following questions.

GREENHOUSE EFFECT

NITROGEN CYCLE

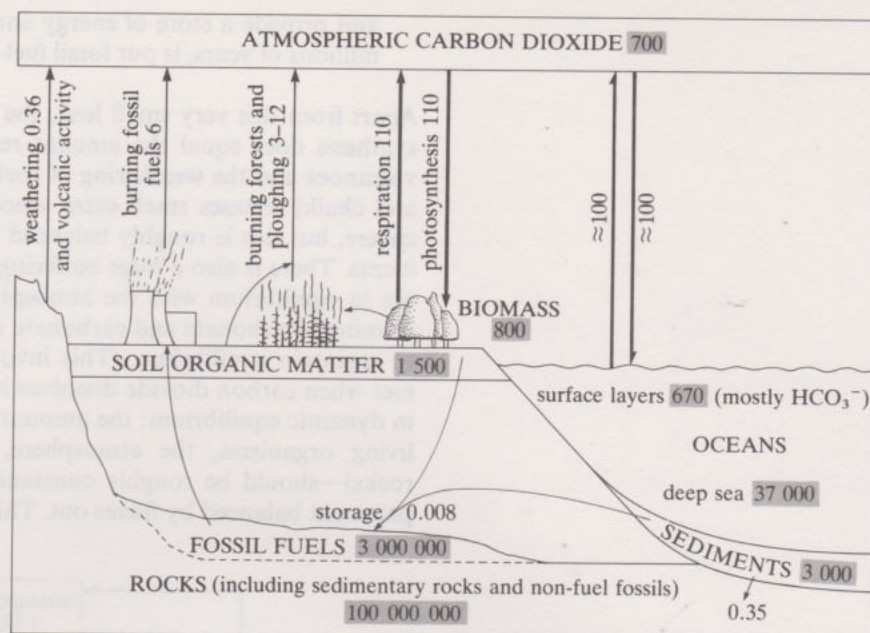


FIGURE 13 The complete carbon cycle showing carbon dioxide inputs to the atmosphere from human activities. Fluxes of carbon (along arrows) are in 10^9 tonnes yr^{-1} , and quantities of carbon in compartments are in 10^9 tonnes.

- ☐ Which compartment contains the greatest amount of carbon and what chemical forms is it in? How much carbon moves into and out of this compartment?
- ☒ Most carbon is in the rocks, which contain over 10^{17} tonnes of it. This includes the fossil fuel reserves (consisting of organic carbon) and all the fossils and compressed sediments (which are mainly calcium carbonate). There are just two small inputs of carbon to this compartment: 0.35×10^9 tonnes per year from deep sea sediments as they are slowly converted to sedimentary rock; and 0.008×10^9 tonnes per year from organic carbon in soil or sediments to the fossil fuel reserves. The only *natural* outputs are carbon dioxide from the weathering of carbonate in rocks (which was mentioned earlier) or from volcanoes. But nearly 20 times more carbon dioxide is released from the burning of fossil fuels.
- ☐ When forests are burned and soils ploughed for agriculture, which stores of carbon are being depleted?
- ☒ Burning depletes the store of organic carbon in living organisms, mainly in plant biomass. And ploughing depletes the store of organic carbon in the soil. You may have been surprised to see in Figure 13 that there is almost twice as much organic carbon in the soil as in living plants and animals.

So human activities are shifting organic carbon from fossil fuels, biomass and the soil into the atmosphere as carbon dioxide. What effect does this have? Initially it had very little: for many years it appears that the huge oceanic reservoir exerted a homeostatic effect, mopping up excess carbon dioxide from the atmosphere. More recently, as the rate of carbon dioxide release has increased, the flux into the oceans has not kept pace. Currently only half to two-thirds of the excess carbon dioxide is being mopped up and the consequence is, as you might expect, that the atmospheric concentration of carbon dioxide is steadily increasing. This is shown clearly in Figure 14.

The peak and trough that occurs each year is a striking demonstration of increased primary productivity in summer (lower carbon dioxide levels) and decreased productivity but continuing respiration in winter (higher carbon dioxide levels). The gradual trend from 315 p.p.m. (parts per million by volume) in 1958 to 340 p.p.m. in 1980 is almost certainly the consequence of human industrial and agricultural activity—burning and forest clearing, in

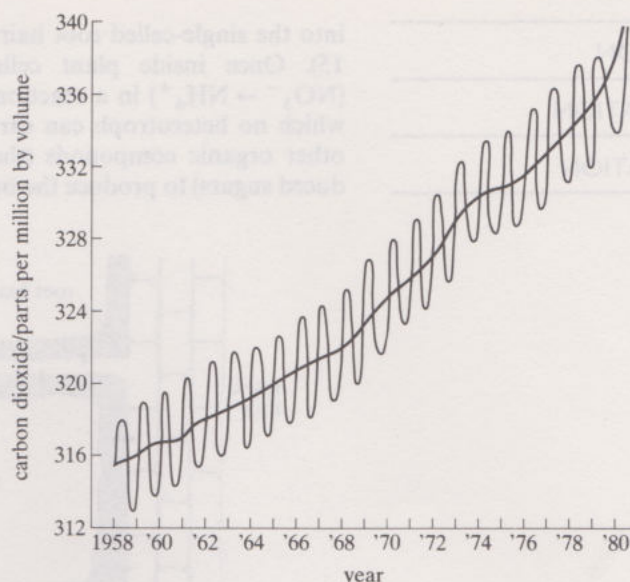


FIGURE 14 Increasing atmospheric concentration of carbon dioxide as recorded at the Mauna Loa Observatory in Hawaii.

short. In the 19th century the comparable figure was 290 p.p.m., and forecasts for the turn of the century range between 375 and 400 p.p.m. (depending on what is predicted for the homeostatic effects of the ocean). Concern over this phenomenon centres on the increased absorption of solar infrared radiation in the atmosphere, by the raised concentration of carbon dioxide (and other gases released through human activities), causing a rise in average global temperature. This is called the **greenhouse effect**, and current debate focuses (very reasonably) on the possible consequences of such a temperature change. These include not only changes in climate, particularly rainfall, but also a rise in sea-level as water stored in the polar ice caps is mobilized and as seawater warms up and increases in volume. One prediction, made in 1987, is that by the year 2025 the greenhouse effect will raise the average global temperature by 0.6–1.0°C, with a concomitant rise in sea level of 4–8 cm due to thermal expansion of the oceans (excluding any effects from melting polar ice).

The difficulties of measuring changes on this scale, and the consequently large variations in estimates between authorities, prevent general acceptance or dismissal of such predictions. The issue, however, is a major one of the many environmental problems that are increasingly entering the realm of popular and political awareness.

3.2 THE NITROGEN CYCLE

The biogeochemical **cycle of nitrogen** is also linked with several major environmental issues, which will emerge later as we describe the cycle. Nitrogen is needed by all living organisms because, as you know from Unit 22, it is a component of many vital compounds in cells. Proteins and nucleic acids are two particularly important examples. However, plants and animals obtain nitrogen in different ways. The source of nitrogen for green plants and most other autotrophs is inorganic ions in the soil or water—either the nitrate ion (NO_3^-) or, less commonly, the ammonium ion (NH_4^+). Crops grow poorly if the soil is deficient in these ions, and this is why they are so often supplied in fast-acting fertilizers. By contrast, animals and many microbial heterotrophs obtain nitrogen only from organic molecules.

What happens in a typical plant is that nitrate ions in solution move from the film of water that surrounds soil particles into young roots, particularly

NITRIFICATION

EUTROPHICATION

DENITRIFICATION

into the single-celled root hairs that stick out from the root surface (Figure 15). Once inside plant cells, nitrate is reduced to ammonium ions ($\text{NO}_3^- \rightarrow \text{NH}_4^+$) in a reaction that requires a lot of metabolic energy and which no heterotroph can carry out. The NH_4^+ is then incorporated into other organic compounds (themselves made from photosynthetically produced sugars) to produce the building blocks of proteins and nucleic acids.

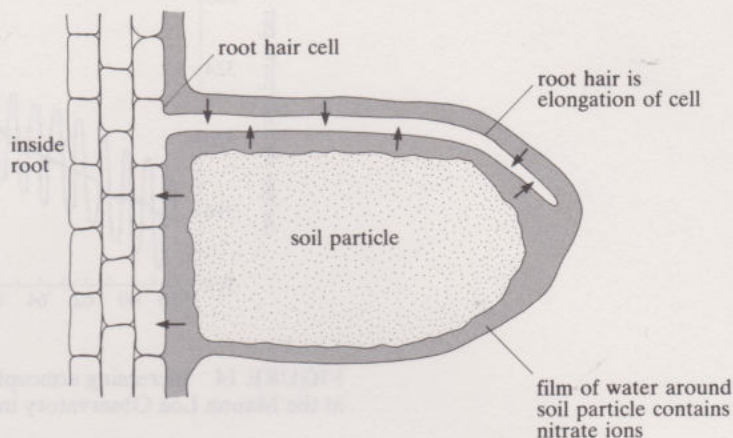


FIGURE 15 Movement of nitrate ions, NO_3^- , (indicated by arrows) from the soil solution into a root hair and the outer cells of a root.

Just as the energy and organic carbon needs of herbivores, carnivores, detritivores and decomposers are supplied (directly or indirectly) by plants, so is their need for organic nitrogen. *Provided that* organic nitrogen in dead tissues, dung etc. can be converted back into inorganic nitrate, we can now write the simple version of the nitrogen cycle shown in Figure 16.

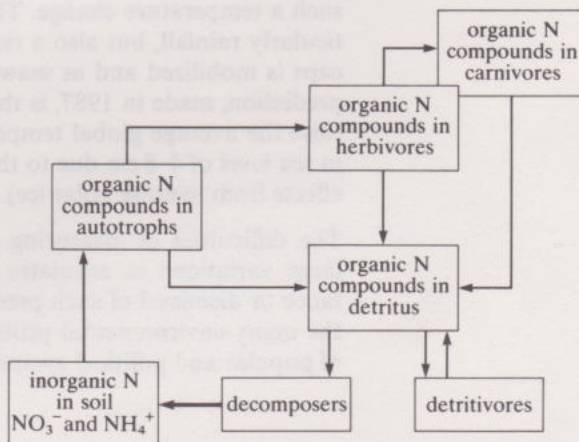
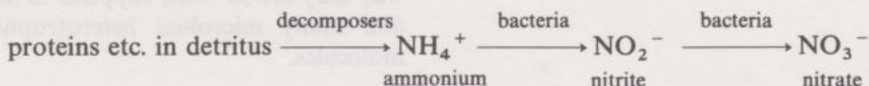


FIGURE 16 The biological part of the nitrogen cycle. (See text for the significance of the thicker arrow.)

The thick arrow in Figure 16 represents several important steps. First, the bacterial and fungal decomposers break down organic nitrogen in detritus to release ammonium ions. If there is no oxygen available or if the soil is very wet, cold or acidic, the process stops here and only NH_4^+ ions will be available to plants. But in 'good' soil conditions, the NH_4^+ is converted by other soil bacteria to nitrite ions (NO_2^-) and then by another group to nitrates (NO_3^-). In short:



Conversion of ammonium to nitrate in this way is called **nitrification**.

The reservoir of inorganic nitrogen in the soil or water is usually quite small, so unless it is constantly 'topped up' by decomposition and the nitrification process, it would be depleted.

fication process, plants rapidly deplete the soil of nitrogen salts. Unlike the mineral cycle shown in Figure 10, and discussed at the beginning of this Section, the reservoir of nitrogen in rocks is comparatively small. This is one reason why the nitrogen available to plants within an ecosystem is all too easily depleted: the harvesting of plants or the movement of animals or detritus from the system is equivalent to a major 'leak' in the cycle.

- ☐ From your general knowledge, how are the losses from this leak replaced in agricultural ecosystems?
- Nitrogenous fertilizers are applied to the soil. These may be manure or compost (replacing the missing detritus) or inorganic nitrogen salts (directly replacing the soil inorganic nitrogen).

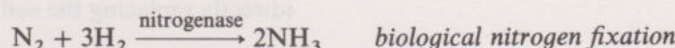
The nitrogen cycle is also vulnerable to two other sorts of leak, one of which is leading to serious environmental problems. This leak arises because nitrate salts are very soluble in water and, unlike other soil ions, do not bind tightly to soil particles. So nitrates are easily washed out of soil by heavy rain in a process called *leaching*. All ecosystems, except those in very dry areas, lose some nitrogen in this way. Rainwater percolating through the soil carries leached nitrogen to rivers and eventually away to sea. The loss is small if nitrates formed in or added to the soil are quickly taken up by plant roots, and this is what happens in undisturbed forests, for example. But the loss can be very large if the ground has become clear of plants or if a large excess of inorganic fertilizer has been added.

Unfortunately, large losses are occurring for these reasons in many parts of the world. Forest clearance in the tropics, for example, destroys a system that is far more efficient at retaining soil nitrogen than any crops planted subsequently; as a result of ploughing and thin plant cover, heavy rainfall rapidly depletes the soil of nitrogen and the land becomes unproductive. Tropical farmers can rarely afford to replace all this nitrogen with fertilizers but farmers in temperate regions often can and do. However, efforts in developed countries to boost crop yields have caused far *too much* inorganic nitrogen to be applied, only about a third of which can be taken up by the crop. The rest is leached and, apart from the obvious wastefulness of this, leached nitrates are a positive nuisance. First, they contaminate water used for drinking, and above a low level nitrate is toxic to humans—especially babies. This is already a problem in some eastern English counties, and babies there are often provided with purified bottled water. Second, leached nitrates and nitrates in treated sewage effluent contribute to the problem of excessive growth of algae. You may have seen lakes looking like pea soup and rivers choked with blanket weed (caused by unicellular and filamentous algae, respectively). This **eutrophication**, as it is called, is a direct result of having too much nitrate (from run-off and treated sewage) and too much phosphate (mainly from treated sewage) in the water. Excess phosphate is the more important cause of eutrophication in freshwaters. Nitrate and phosphate ions are nutrients that stimulate the growth of certain algae. The result is not only unsightly to us but also dangerous to fish: respiration by the huge populations of algae at night sometimes removes all the oxygen from the water and, when the algae die, toxic metabolites may be released. Some lakes are *naturally* eutrophic, with luxuriant algal growth, and eutrophication caused by sewage effluents and fertilizers is really an exaggerated form of a natural phenomenon. There is also some evidence that nitrate entering the North Sea from rivers is causing excessive growth of marine phytoplankton, and the primary cause of eutrophication in this instance is nitrate not phosphate.

Apart from leaching, the other leak in the nitrogen cycle arises because both ammonia (NH_3) and molecular nitrogen (N_2) are gases. Ammonia readily forms from ammonium ions, especially in warm conditions, and if this happens in soil, ammonia escapes into the atmosphere. Soil nitrates can be lost as nitrogen gas (or as gaseous oxides of nitrogen) if the soil becomes waterlogged and anaerobic. The process of **denitrification** occurs under these conditions through the activity of denitrifying bacteria, which reduce nitrates (NO_3^-) to nitrites (NO_2^-) and then to oxides of nitrogen or nitrogen gas (N_2). In marshes or wet 'heavy' soils, quite a lot of soil nitrogen is lost in this way.

NITROGEN FIXATION

These potential leaks—harvesting or export, leaching, loss of ammonia and denitrification—mean that the nitrogen cycle is vulnerable and there must be mechanisms for topping it up. It is all very well for humans to do this by supplying fertilizers to managed ecosystems, but what happens in unmanaged ('natural') ecosystems? The answer is biological **nitrogen fixation**. This is a biological version of the Haber-Bosch process (Unit 16), the industrial process that reduces atmospheric nitrogen gas to ammonia, which is used in fertilizers. Nitrogen-fixing organisms carry out the same reaction—but a lot more efficiently—using the nitrogenase enzyme described in Unit 22. All the biological nitrogen fixation on the planet is probably mediated by no more than a few kilograms of this enzyme!



Only certain bacteria can fix nitrogen gas so, ironically, other organisms live surrounded by a huge reservoir of atmospheric nitrogen that they cannot use. Many nitrogen-fixing bacteria are free-living in soil or water and they use the fixed nitrogen to manufacture their own proteins etc. Only when these organisms die and their cells decompose do they contribute to the pool of inorganic nitrogen in the soil. Other nitrogen-fixing organisms (for example, the root-nodule bacteria of plants such as beans and clover) live inside plant tissues, and ammonium ions (NH_4^+) pass directly from bacteria to plant; this is equivalent to having a built-in fertilizer factory!

There is also a contribution to the nitrate pool from reactions between atmospheric nitrogen and oxygen, which are a consequence of lightning and other electrical and photochemical effects. The nitrogen oxides produced in this way (plus those released during the burning of fossil fuels) are further oxidized to nitric acid, which is neutralized in soil to give nitrates. Globally, the ratio of biological fixation: atmospheric fixation: industrial (Haber-Bosch) fixation is of the order of 13:3:5. Biological fixation is, therefore, the most important topping-up process in the biogeochemical cycle of nitrogen, but the contribution from industrial fixation is, nevertheless, a significant fraction of the whole.

Figure 17 summarizes the nitrogen cycle and allows you to compare it with the carbon cycle in Figure 12.

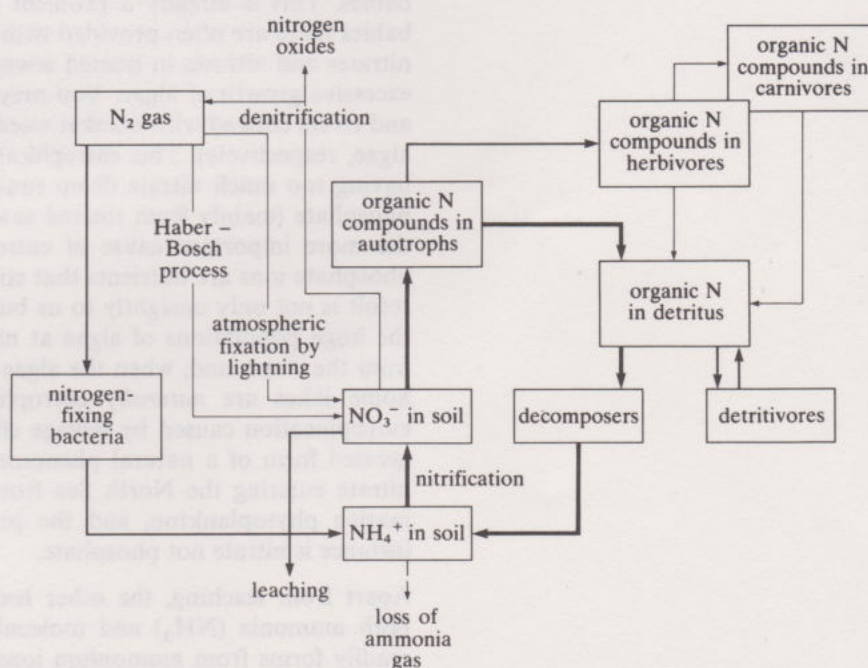


FIGURE 17 The complete nitrogen cycle. (Thickness of line indicates roughly the amount of nitrogen transferred.)

One difference between the carbon and nitrogen cycles is that carbon enters the atmosphere (as CO_2) at every turn of the cycle, whereas atmospheric nitrogen is not an integral part of the core nitrogen cycle. Nitrogen can be thought of as cycling between inorganic soil nitrate and the organic nitrogen compounds of cells, with fixation providing a substantial 'top-up' that compensates for leaching, denitrification and loss of ammonia. Human mismanagement of ecosystems, coupled with the need to grow more food, are the basic reasons for the nitrogen-related problems described in this Section. Ecosystems have been disturbed, so nitrogen losses through leaching far outstrip the inputs; and over-compensation for losses, when trying to increase crop yields, has led to water pollution and a waste of the nitrogen expensively produced by industrial fixation.

3.3 THE PHOSPHORUS AND SULPHUR CYCLES

At the beginning of Section 3 we distinguished between biogeochemical cycles, which all elements have and which are studied globally, and mineral cycles, which can be studied within ecosystems. The carbon cycle is clearly a biogeochemical cycle but the nitrogen cycle is something of a hybrid: although the core cycle can be localized, nitrogen fixation and denitrification involve the atmosphere. Now we shall consider a typical mineral cycle, that of phosphorus, and mention briefly another hybrid cycle, that of sulphur. You can see from Table 5 that both these elements are macronutrients (that is, they are needed in relatively large amounts by living organisms) and you know from Unit 22 that both are vital components of cells (phosphorus is a constituent of nucleic acids, and sulphur is a constituent of some proteins, for example).

Phosphorus is taken up by plants as phosphate ions and then cycles in the same way as shown for nitrogen in Figure 16. However, it is a remarkably tight cycle. Very little phosphate is lost by leaching because phosphate ions are virtually immobile in soil: they bind to soil particles and also form insoluble compounds (in striking contrast to the behaviour of nitrate ions). This is the positive side of phosphate immobility, but there is also a negative side. Bound phosphate is unavailable to plants, so they are often short of phosphorus when the soil contains plenty of phosphate. This problem is particularly bad in strongly acidic or alkaline soils. For good crop growth extra phosphorus must usually be supplied by fertilizers, in either an organic or an inorganic form. Another aspect of phosphate immobility is its usefulness to archaeologists. Many animal tissues and wastes, including bone, urine and faeces, are rich in phosphorus, and at sites where these are concentrated the level of soil phosphate rises and stays high for a long time; human dwelling sites that are several thousand years old have been identified by measuring the amounts of soil phosphorus.

Urban societies no longer put their phosphorus-rich wastes back into the soil. Instead, we let bacteria in sewage works do the job of soil decomposers and, having thus made the phosphate soluble, we pump it out with sewage effluent into rivers, lakes or the sea. In effect this introduces a leak into the land-based phosphorus cycles and is the primary cause of the eutrophication problem mentioned in Section 3.2. Interfering with mineral cycles really can cause problems and we are only just beginning to understand what they are. This is certainly true for the sulphur cycle.

The core sulphur cycle is also much as shown for nitrogen in Figure 16, with alternation between organic and inorganic sulphur and uptake into plants as the sulphate ion. Unlike phosphorus (but like nitrogen), the sulphur cycle is naturally leaky: sulphate leaches quite easily from soil and certain products of sulphate decomposition are gases, which escape into the

atmosphere, where they are converted to sulphur dioxide. A large proportion of these gases derives from marine phytoplankton. The cycle is completed when atmospheric sulphur compounds are returned to the ground in rainwater. Interference through human industrial activity is significant here, because when fossil fuels (which contain quite a lot of sulphur) are burnt, a large amount of sulphur dioxide gas is released. As a result the amount of sulphur entering the atmosphere has increased by around 40 %. When all this sulphur returns to the ground in rainwater, it contributes very substantially to another major environmental problem: acid rain.

3.4 ACID RAIN

There is now clear evidence that the pH of rain falling in parts of Europe and North America is lower than it used to be, and there is great concern about the biological effects of this acid rain. Rain of pH 4 or even lower now falls in areas where pH 5 or higher has been the norm. Since pH is a logarithmic scale, rain of pH 4 has *ten times* the hydrogen ion concentration of rain of pH 5.

Chemically, the increased rain acidity is a consequence of the emission of sulphur and nitrogen oxides into the atmosphere. As you saw in Unit 15, sulphur dioxide is converted in the moist atmosphere to sulphuric acid (H_2SO_4), and nitrogen oxides (e.g. NO) are similarly oxidized to nitric acid (HNO_3). Both of these are strong acids that lower the pH of rain. The gases derive mainly from burning fossil fuels but natural processes also contribute, and human activities may be increasing this component too. For example, we mentioned in Section 3.2 that excess nitrates from fertilizer use and sewage appear to be stimulating the growth of phytoplankton in the North Sea, and in Section 3.3 that the metabolism and decomposition of such algae leads to sulphur dioxide formation in the atmosphere. What this means is that some—and it could be as much as 30 %—of the sulphur dioxide reaching continental Europe from air passing over the North Sea could derive from increased algal growth.

The question that concerns us here is what does acid rain *do* to ecological systems and, in particular, is it responsible for dramatic and distressing changes such as the decline in fish populations in Scandinavian waters and the 'forest decline' in central Europe? Taking the fish problem first, consider the following facts, which relate to a group of Scandinavian lakes:

- (a) The pH of lakes on granite bed rock fell by an average of 0.45 pH units between the average for the period 1929–53 and the average for the mid 1970s.
- (b) Fish populations in some lakes began to decline from about 1960.
- (c) Good fish populations usually occur only in lakes with a pH above 5.3.

☐ How do you relate these facts to acid rain?

☒ A possible relationship is that acid rain has *caused* the decline in lake pH which, in turn, has *caused* a decline in fish populations.

Both of the causal links in this answer involve assumptions. The first is indeed true—acid rain *is* the cause of increased lake acidity—but only lakes surrounded by acidic soil show this fall in pH. The second assumption is *not* strictly true, however. Further work has shown that fish die in acidic waters only if the level of calcium is low and, especially, if aluminium levels are high. It turns out that as acid rain percolates through soil, hydrogen ions (H^+) displace aluminium ions (Al^{3+}), which leach out into rivers and lakes and are toxic to fish. So acid rain is responsible for the fish decline but mainly through its effects on soil and not simply by lowering the pH of lakes.

Forest decline is an even more complex problem, which was first detected in 1980 and is now (1987) affecting at least seven European countries, from northern Italy to southern Sweden (and is possibly beginning to appear in the UK). It affects mainly conifers, although beech and oak are now showing some symptoms, is most common at high altitudes, and usually

causes first yellowing then shedding of leaves, followed by tree death. In 1986 about 50 % of the forest area in West Germany was damaged to some degree, and this is clearly a major ecological catastrophe. Is it caused by acid rain? The answer seems to be that acid rain contributes to forest decline but is not the sole culprit. Ozone, which is produced in the lower atmosphere by reactions involving nitrogen oxides and hydrocarbons, appears to be another factor involved, and there could be others.

Debate now centres not on whether to reduce emissions of sulphur dioxide from power stations but on how rapidly it should be done, which boils down to a question of how much countries are prepared to spend. The problem is compounded when, as often happens, the pollutants emitted from tall chimneys in one country are washed down in rain on another country. What to do about nitrogen oxide and ozone pollution is less clear and what, if anything, can be done to restore soils leached by acid rain, and freshwaters acidified and contaminated by aluminium ions is also uncertain. Adding limestone (calcium carbonate) to lakes and soils is one approach that is being tried but this may not provide a long-term solution. It also involves yet more interference with biogeochemical cycles and, until we know much more about how these cycles operate, this is a risky thing to do on a large scale.

SUMMARY OF SECTION 3

1 All elements of importance to living organisms cycle between living and non-living compartments (soil or sea, rocks and atmosphere). On a global scale these are called *biogeochemical* cycles. Cycles that do not involve the atmosphere are localized within ecosystems in the short term and are called *mineral* cycles.

2 Localized cycles are never completely closed: they 'leak' for a variety of reasons (e.g. as a result of leaching of soil by rain) and there are various ways in which this loss is replaced (e.g. by weathering of rocks).

3 The carbon cycle is a biogeochemical cycle. In the biological part of the cycle, carbon enters plants as carbon dioxide and is converted photosynthetically to organic compounds. Organic carbon and energy move together from plants to herbivores, carnivores, detritivores and decomposers through the normal food webs. Globally, virtually all organic carbon is re-converted to carbon dioxide during respiration, except for a small fraction, which is stored in peat or sediments. This stored carbon eventually forms fossil fuel in the rock compartment.

4 Carbon dioxide taken up in photosynthesis roughly balances that released in respiration. However, two other processes make a substantial net input of carbon dioxide to the atmosphere: burning fossil fuels, and burning forests and ploughing the cleared land.

5 The oceans act as a carbon dioxide buffer and remove part, but not all of the extra carbon dioxide entering the atmosphere. Consequently, there has been a progressive increase in the concentration of atmospheric carbon dioxide over recent decades. This contributes to a greenhouse effect, which causes the average global temperature to rise.

6 On a local level (within an ecosystem), nitrogen cycles between organic nitrogen compounds in living organisms or detritus, and inorganic nitrogen (nitrate and ammonium ions) in soil or water. Plants take up inorganic nitrogen and convert it to organic nitrogen, which is transferred to heterotrophs through food webs. Decomposers release ammonium ions (NH_4^+) from detritus and, in suitable conditions, these are converted to nitrates (NO_3^-) by nitrifying bacteria (in the nitrification process).

7 This core part of the nitrogen cycle is intrinsically leaky because (a) the nitrate ion is extremely soluble and, on land, is easily leached from the soil; and (b) nitrate and ammonium ions may be lost to the atmosphere (the first as nitrogen gas in the process of denitrification and the second as ammonia gas).

POPULATION DENSITY

8 The nitrogen is replenished by nitrogen fixation, which is the reduction of atmospheric nitrogen gas to ammonia. Biological fixation is carried out by bacteria and, globally, this is the major topping-up process for the nitrogen cycle. Atmospheric fixation (by lightning) supplies about 25 % as much nitrogen as biological fixation, and industrial fixation supplies about 40 % as much (but all this enters agricultural ecosystems as fertilizer).

9 Disturbance of ecosystems by human activities is increasing the loss of nitrates through leaching. Excessive application of industrially fixed nitrogen (fertilizer), most of which is lost by leaching, is contaminating drinking water with nitrate and contributing to the problem of eutrophication.

10 Phosphorus cycles between organic phosphorus compounds in living organisms and inorganic phosphates in soil or water. There are few leaks from this mineral cycle because phosphate ions are highly immobile in soil. However, transfer of soluble phosphates in sewage effluent to freshwater is the primary cause of eutrophication of freshwaters.

11 Sulphur cycles between organic sulphur compounds in living organisms and inorganic sulphate in soil or water. Gaseous products of decomposition escape into the atmosphere and form sulphur dioxide (SO_2).

12 Additional atmospheric inputs of sulphur dioxide and nitrogen oxides from the burning of fossil fuels are contributing to the acid rain problem. Through its effects on soil and freshwater, acid rain is the main factor causing fish populations to decline in some areas. Forest decline appears to result from complex interactions between acid rain and ozone.

SAQ 6 Which of the following types of organism are essential for the cycling of nitrogen and why: (i) green plants; (ii) herbivores; (iii) nitrogen-fixing bacteria; (iv) denitrifying bacteria; (v) decomposers?

SAQ 7 Which of the following activities, (i)–(iii), (a) interferes with the cycling of carbon, nitrogen, phosphorus or sulphur? (b) contributes to the greenhouse effect, eutrophication or acid rain?

- (i) burning coal;
- (ii) flushing the lavatory (after using it);
- (iii) clearing an old woodland and ploughing up the soil.

SAQ 8 Before World War II, it was common for farmers in the UK to rotate their crops. Four crops were grown, and the land was divided into quarters, one quarter for each crop. Each year over a period of four years, each quarter was sown with a different crop. This followed a sequence such that after four years each field would have had all four crops grown on it. The crops were root crops (e.g. turnips, mangolds), barley, clover mixed with grass, and wheat. The root crops were fed to stock (cattle, pigs, sheep) during the winter, often in the field. The clover–grass mixture was either made into hay and fed to stock over the winter or was ploughed into the soil. Barley was harvested mainly for stock feeding, wheat for human food. Explain how this rotation conserved the farm's resources of mineral salts.

SAQ 9 Off the coast of Peru, there is an area of sea where there is usually a very rich growth of phytoplankton that forms the basis of the food chain:

phytoplankton → zooplankton → anchoveta (fish) → guano birds

The guano birds roost on islands and their droppings form a rock that is very rich in phosphates. There are very large numbers of anchoveta, which can be caught easily in nets. Suggest two ways in which the Peruvians could exploit the marine ecosystem to increase world food supplies. Which would you recommend?

4 ECOLOGY OF POPULATIONS

Up to now we have treated organisms mainly as converters of energy and processors of chemical elements. This physical view of ecosystems is all very well, but it ignores one of the most fundamental characteristics of living organisms—their propensity to *reproduce* and so to increase in number. The biogeochemical cycles discussed in the last Section all involve large numbers of organisms of different kinds. You will remember from Section 1 that the number of individuals of a particular species found living together in a particular place is called the population of that species. This Section is about populations in ecosystems: about how they interact and, by interacting, how the **population density** of each species (i.e. the number of individuals per unit area or per unit volume) increases or decreases with time.

4.1 CHANGES IN POPULATION DENSITY

Changes in population density are important and interesting. The choking algal bloom that can occur in lakes and streams as a result of eutrophication is an example of a rapid population increase. In some circumstances, such growth can equally rapidly diminish, as the curve in Figure 18a shows.

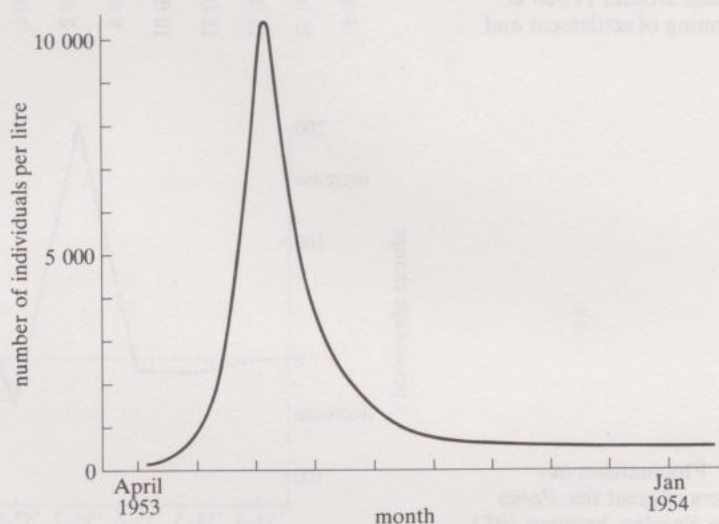


FIGURE 18a The changes in a population of the brown alga, *Dinobryon divergens*.

We can look to animal husbandry for another example: the introduction of free-grazing livestock into a limited area often leads to a population growth that eventually reaches an undulating plateau. Figure 18b shows what happened when sheep were introduced into the island of Tasmania in 1814.

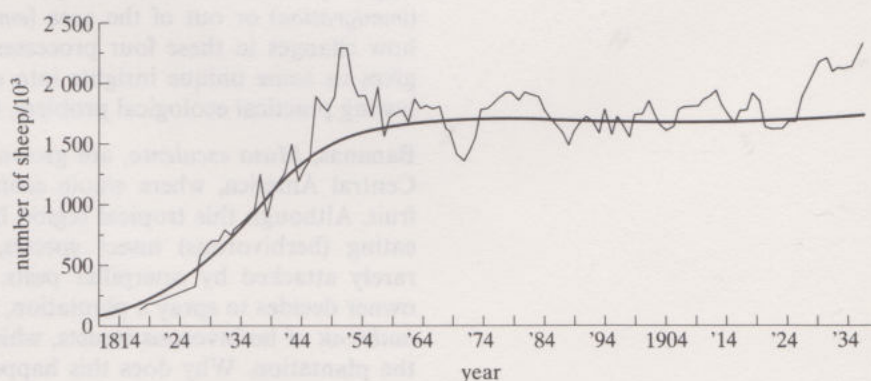


FIGURE 18b Changes in a population of sheep following their introduction into Tasmania, in 1814. The heavy line shows the trend in population size; and the fine lines shows year-to-year variation.

PARASITOID

Another example of a drastically changing population is that of our own species, but an informed discussion of the topic is beyond the scope of this Unit. You can see in Figure 18c that since the time humans began to live in settlements (about 13 000 years ago), world population has increased from less than five million to more than five thousand million. Finally, in Figure 18d, you can see an example of continuous variation in a population of the great tit, *Parus major*.

FIGURE 18c The J-shaped curve of human population growth. There is a slight dip around 1350 AD when an estimated 75 million people died in Europe as the result of bubonic plague. The slight increase around 11 000 BC marks the beginning of settlement and cultivation.

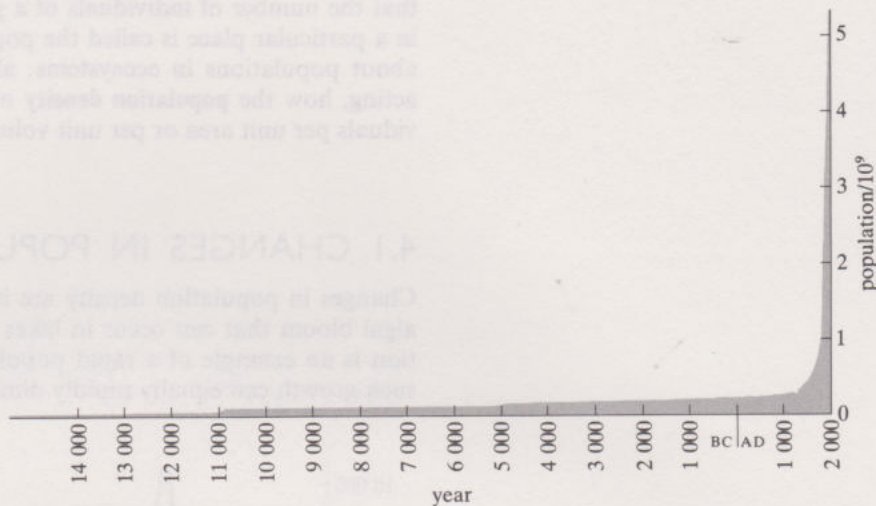
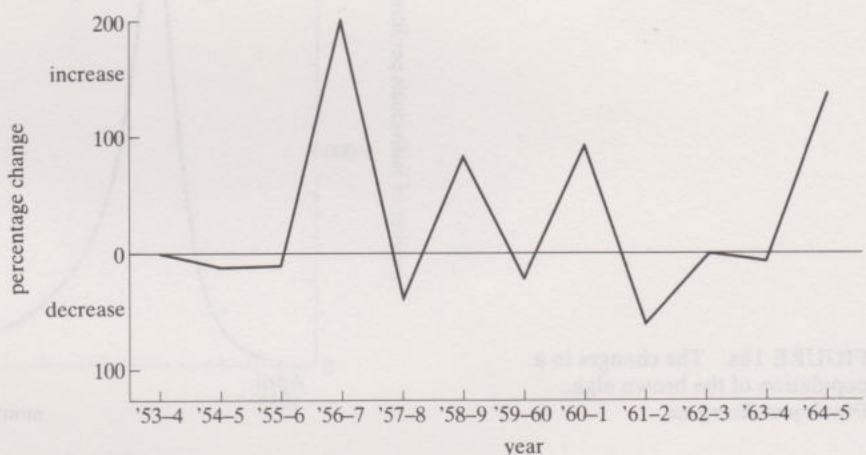


FIGURE 18d Fluctuations in breeding numbers of great tits, *Parus major* in Veluwe, Sweden, between 1953 and 1965.



All these examples illustrate changes in population density. Changes in the number of individuals in a population can be caused in only four basic ways: by births or deaths, or by the movement of individuals into the area (immigration) or out of the area (emigration). Population ecology is about how changes in these four processes affect the size of populations, and it gives us some unique insights into ecological situations. Consider the following practical ecological problem, for example.

Bananas, *Musa esculenta*, are grown in large plantations in many parts of Central America, where whole economies depend on the export of these fruit. Although this tropical region has an enormously rich fauna of plant-eating (herbivorous) insect species, banana plantations are fortunately rarely attacked by caterpillar pests. Despite this, sometimes a plantation owner decides to spray a plantation, 'just in case'. The inevitable result is an outbreak of herbivorous insects, which reach pest proportions and damage the plantation. Why does this happen? By analysing how bananas, herbivore populations and populations of insects that attack herbivores interact, ecologists have provided a simple explanation for this seemingly paradoxical situation.

A banana plantation is a simple community with three trophic levels, consisting of bananas, herbivorous insects and parasitoids. Parasitoids are

insects that lay their eggs in a developing stage of another insect species; the parasitoid larva feeds upon its victim from within, eventually killing it. Let's think about some of the factors that determine the number of births and deaths of herbivorous insects and parasitoids. Taking the herbivorous insects first:

Births will increase when the number of adults increases, if there is plenty of food (banana plants) available.

Deaths will decrease when the number of parasitoids decreases.

When there is an increase in births that is not balanced by an increase in deaths, or there is a decrease in deaths that is not balanced by a decrease in births, the size of the herbivore population will rise. For the sake of simplicity we shall ignore the possibility of immigration or emigration affecting population size. Now let's consider parasitoid populations. In these populations *births* will probably decrease when the number of herbivorous insect hosts decreases. Finally, let's look at the effect of insecticide on the two populations.

- ☐ What will happen to the number of *deaths* of herbivores and of parasitoids when insecticide is sprayed upon this community?
- Initially, a proportion of both populations will be killed by the direct effect of the pesticide, so deaths of both will rise. However, the death of parasitoids *then* causes a *drop* in the number of deaths among the remaining herbivores and their offspring. The net effect of spraying herbicide may therefore be to increase the number of parasitoid deaths while *reducing* the overall deaths of herbivores.
- ☐ What will happen to the number of *births* of herbivores and parasitoids when insecticide is sprayed upon this community?
- Initially, the births of both will decrease because adults of both herbivores and parasitoids will be killed. Later there will be a greater proportion than usual of herbivores surviving to lay eggs.

Spraying insecticide on bananas has different effects on populations at different trophic levels. It *decreases* subsequent deaths among those herbivores that survive the spraying, and they are soon able to increase their numbers because their food is very abundant and they are less parasitized. Insecticide has a double effect upon parasitoids, which initially suffer a decrease in births as well as an increase in deaths. If pesticide spraying is stopped, parasitoid populations will build up their numbers again, but in the meantime there is an outbreak of banana pests.

- ☐ What does the example tell you about how the number of herbivorous insects may be kept low without the use of insecticides?
- Numbers may be kept low by parasitoids.

This is the principle used in the biological control of pests; a subject we shall return to in Section 4.5. Next, however, we should look more closely at why populations fluctuate.

4.2 THE CAUSES OF POPULATION FLUCTUATIONS

Populations are composed of living individuals whose numbers fluctuate according to fluctuations in births and deaths. To understand what causes a plague of locusts, or a sudden increase in thistles, or field voles, we have to find out what the causes of changes in births and deaths are. For example, the dramatic increases in the number of great tits shown in Figure 18d followed bumper crops of the beech seeds upon which they feed in Sweden. Following a bumper crop, the extra available food reduced the number of deaths of juvenile tits, which normally occurred during winter. More birds

NATALITY RATE

MORTALITY RATE

DENSITY-DEPENDENT
MORTALITY RATE

DENSITY-INDEPENDENT
MORTALITY RATE

MORTALITY FACTOR

survived to the following spring, and their numbers increased the size of the population. This relationship between the beech seed crop and number of great tits is shown in Figure 19.

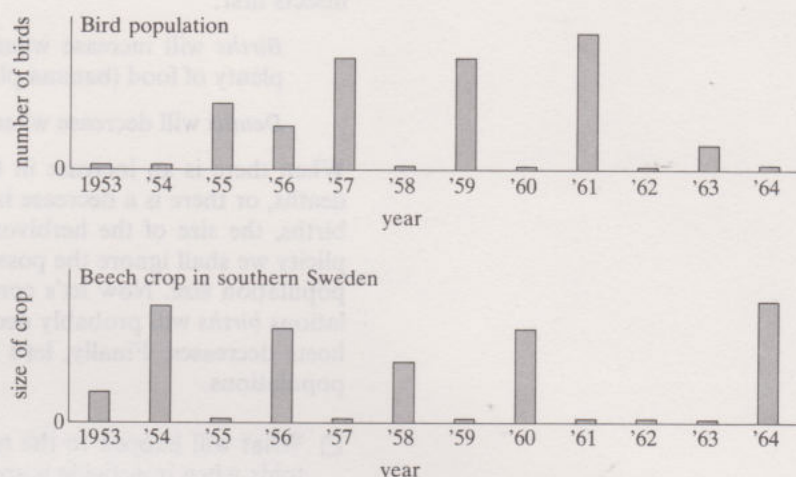


FIGURE 19 Irruptions in breeding numbers of great tits, *Parus major*, and the size of the beech crop. Irruptions occur in the years following large beech crops.

When a population 'explodes' in number because of a dramatic decrease in deaths or increase in births, the population density rises. In certain animal species the population spills out into other areas in periods of emigration called *irruptions*. In Europe a number of seed-eating birds such as crossbills, show periodic irruptions.

- ☐ Why are populations of seed-eating birds particularly prone to irruptions?
- ☒ Their food supply fluctuates considerably from year to year, and this causes changes in their population density. When a period of food abundance is followed by a period of shortage, highly mobile animals such as birds tend to emigrate, i.e. irrupt.

As you saw in the discussion of fecundity in Unit 19, populations are inherently capable of rapidly increasing in numbers. The weed, fat hen, *Chenopodium album*, can produce 400 000 seeds in a year. Obviously, this prodigious fecundity cannot be translated directly into population growth or the world would very soon become overrun with fat hen. What prevents this happening in natural populations? Once again the answer is, at least in principle, quite simple. Population size may be limited by increases in mortality (deaths) or decreases in natality (births) as the population increases. Up to now we have talked of births and deaths as though they were absolute numbers, like the numbers of births and deaths recorded in a newspaper, which just tell you that there have been so many deaths and so many births associated with readers of that paper. A much more useful figure is the number of births *per adult* member of the population, or the number of deaths per adult. These figures are called the birth rate or **natality rate** and the death rate or **mortality rate**. For example, a mortality rate of $\frac{1}{100}$ (or 1%) would represent one death in a population of 100, and ten deaths in a population of 1 000.

Death rates and birth rates that change with population density are described as **density-dependent mortality rates** and density dependent natality rates, respectively. These have the important property that they can prevent populations increasing any further in size when they are already at a high density.

For example, in Wytham Wood, near Oxford, the death rate of newly fledged owls (owlets that have just left their nests and are seeking to establish themselves) is much greater in years when the wood already has a high owl population. In other years, when the overall population is low, perhaps

because of a severe winter or some other crisis, many more newly fledged owls survive and find nests of their own. Thus the mortality rate (i.e. the percentage of the population that dies) of newly fledged owls is clearly density dependent. Figure 20 uses mortality rates to compare density-dependent and density-independent effects. The dotted line represents a **density-independent mortality rate**: in the case of owls it could mean that a fixed percentage is killed by the winter cold irrespective of the number in the wood. The solid line represents one example of a density-dependent mortality rate. (The line need not be exactly like this to show density dependence; it may be curved or have a different gradient, but it must show that mortality rate is proportional to population density.) If the *solid* line represented the mortality rate of the owls, it would mean that a greater percentage of fledglings are killed (or emigrate) in years when the owl population is higher.

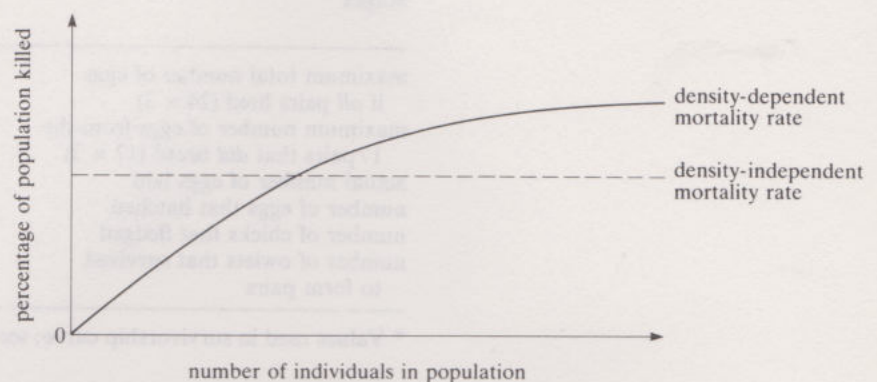


FIGURE 20 Some mortality rates are affected by the density of the population on which they act and some are not.

It is plain from this description that when the mortality rate or the natality rate is density-dependent it will have a *regulating effect* on the population, tending to restore the number in the population towards an average value.

When we look more closely at the factors that affect population density we shall simplify our analysis by, for the most part, ignoring immigration and emigration. You need to remember, however, that these factors exist and can be significant. As for births, you will see shortly that it is usual practice when studying population dynamics to consider a birth rate that is lower than that which is potentially achievable as a kind of mortality. For example, the normal maximum clutch size of the owls of Wytham Wood is three eggs per pair, but under a variety of circumstances this maximum is not achieved, and this affects the population. 'Eggs not laid' is one of the **mortality factors** (i.e. causes of death) in the life cycle, and contributes to the overall mortality experienced by tawny owls in this population. By following a group of owls through their lives from egg to mature adult, we can discover what other mortality factors operate, as birds are lost to the population through a variety of causes.

The kind of detailed work that is needed to gather such data is illustrated by the classic study of the tawny owl population at Wytham Wood that was carried out by H. N. Southern between 1947 and 1959. Within the 525 hectare ($525 \times 10^4 \text{ m}^2$) site, there were—varying over the years—between 17 and 32 pairs of owls, each pair occupying its own, well guarded territory. On average, a pair remained mated and held a particular territory for about five years. Since owls live a long time and breed many times in a lifetime, owl generations overlap. In the spring of each year, *some of the pairs bred*, producing *up to three eggs* in a clutch. In May, *some of the eggs hatched*. Throughout the summer the owlets were fed by the parents and *some survived* to fledging. In autumn, the newly fledged birds sought their own territories with *varying success* (some died, some left Wytham Wood and some established themselves within the wood).

LIFE TABLE

SURVIVORSHIP CURVE

k-VALUE ANALYSIS

k-VALUE

The italics in the previous paragraph show, in a way which does not do justice to the careful experimental work involved, the five mortality factors that operate within one generation. These are (1) 'mortality' as a consequence of failure to breed, (2) 'mortality' as a consequence of failure to produce the maximum number of eggs, (3) 'mortality' through the failure of some eggs to hatch, (4) 'mortality' because some owl chicks die before fledging, (5) 'mortality' because some fledglings fail to secure a territory within Wytham Wood in which to mate and breed. (Here, mortality will include those that fly off to another wood where the owl population is lower and territories are available.) Data for the year 1952-3 are shown in Table 6. This is an example of a **life table**.

TABLE 6 Mortality factors 1 to 5 operating on 24 pairs of owls in Wytham Wood in 1952-3.

Stages	Values of N_0 to N_5	Mortality factor operating (<i>see text</i>)
maximum total number of eggs if <i>all</i> pairs bred (24×3)	$N_0 = 72$	mortality (1): $72 \rightarrow 51$
maximum number of eggs from the 17 pairs that <i>did</i> breed (17×3)	$N_1 = 51$	
actual number of eggs laid	$N_2 = 43^*$	mortality (2): $51 \rightarrow 43$
number of eggs that hatched	$N_3 = 16^*$	mortality (3): $43 \rightarrow 16$
number of chicks that fledged	$N_4 = 15^*$	mortality (4): $16 \rightarrow 15$
number of owlets that survived to form pairs	$N_5 = 9^*$	mortality (5): $15 \rightarrow 9$

* Values used in survivorship curve; see text.

We can use the data in a life table such as Table 6 to plot a graph of the numbers of survivors against time. This is called a **survivorship curve**. For the generation of owls hatched in 1952 we can draw a survivorship curve by taking the asterisked figures in Table 6 and *normalizing* them—that is, by making 43 eggs represent 100% (each asterisked figure is therefore multiplied by $\frac{100}{43}$). When plotted against months in the year 1952-3, the survivorship curve for the first year of life is given in Figure 21a.

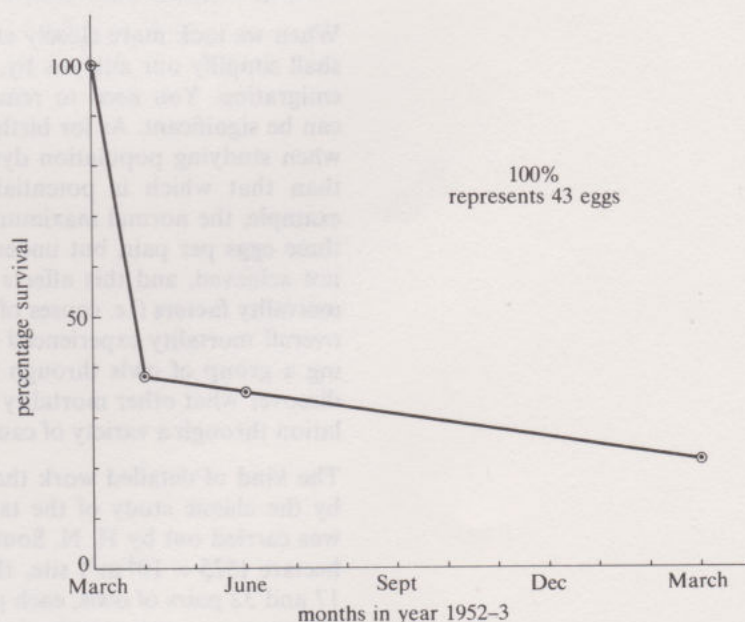


FIGURE 21a Survivorship curve for the eggs and young tawny owls in Wytham Wood in 1952-3.

This is only a partial survivorship curve because owls remain mated and fecund for several years. In fact, in studies over a period of time with a larger population, the curve has the overall appearance shown in the sketch in Figure 21b. You can see that the steepest part of the curve is in year one.

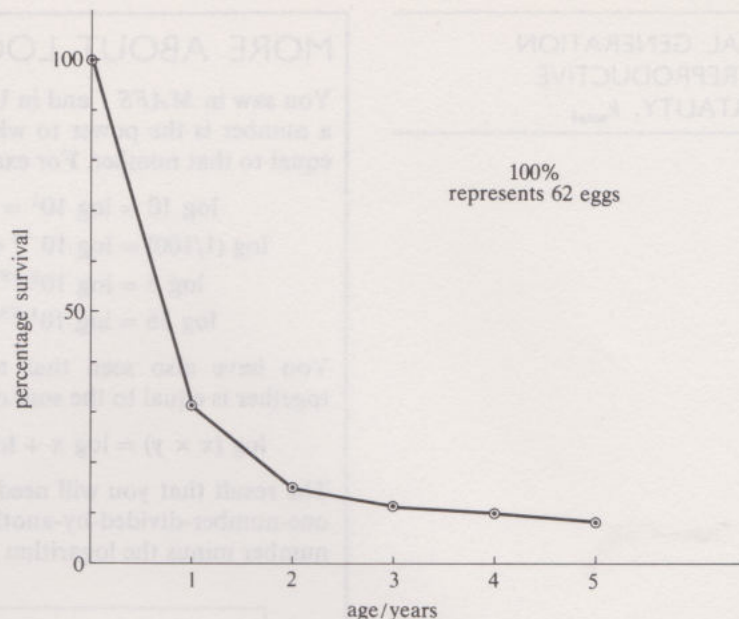


FIGURE 21b Survivorship curve for the eggs and young tawny owls in Wytham Wood over a five year period.

Therefore, the mortalities described in Table 6 have the greatest overall effect in year one.

But, if we ask how much this table tells us about survival and population regulation among Wytham Wood tawny owls, the answer is 'only part of the story'. It is quite clear that overall mortality (from a potential survival of 72, only nine owlets survived to form pairs; see Table 6) is contributed to by five mortality factors. However, it is hard to see which is the most significant—and we have no idea why one should be larger than the other. It is also not clear whether the years 1951–2, 1953–4, 1954–5 and so on would have given the same pattern. And above all, we have not related these mortalities in any way to the life-style (i.e. to the natural history) of the tawny owls themselves. It is to these questions that we turn in Section 4.3.

4.3 MORTALITY FACTORS AND *k*-VALUE ANALYSIS

For reasons that will become clear, one very effective way of examining the sequential effects of the various mortalities that contribute to the overall pre-reproductive mortality is by ***k*-value analysis**. You already know about mortality rates (the percentage of a population that has been killed or has died), and you might perhaps expect the data of the type in Table 6 to have been analysed further in terms of these percentages. However, from *arithmetical* and *experimental* standpoints, a much more useful way of representing 'how much death?' is by calculating ***k*-values** instead of mortality rates. You will have to take this on trust for a moment, while the definition and meaning of *k*-values are made clear.

If N_B owl chicks in Wytham Wood hatched and N_A survived to fledging, the percentage mortality would, of course, be $[(N_B - N_A)/N_B] \times 100$ (i.e. the number dying ($N_B - N_A$), divided by the number present initially (N_B), multiplied by 100). The *k*-value of the owl-chick mortality, however, is given by the expression:

$$k = \log N_B - \log N_A$$

and this is the same as

$$k = \log \frac{N_B}{N_A}$$

(For an explanation, see the box 'More about logarithms' overleaf.)

TOTAL GENERATION
PRE-REPRODUCTIVE
MORTALITY, k_{total}

MORE ABOUT LOGARITHMS

You saw in *MAFS 1* and in Unit 15 that the logarithm to the base ten of a number is the power to which ten must be raised in order to make it equal to that number. For example,

$$\begin{aligned}\log 10 &= \log 10^1 = 1 \\ \log (1/100) &= \log 10^{-2} = -2 \\ \log 5 &= \log 10^{0.6990} = 0.6990 \\ \log 36 &= \log 10^{1.5563} = 1.5563\end{aligned}$$

You have also seen that the logarithm of two numbers multiplied together is equal to the sum of the logarithms of each number, that is

$$\log (x \times y) = \log x + \log y$$

The result that you will need to use in this Unit is that the logarithm of one-number-divided-by-another is equal to the logarithm of the first number minus the logarithm of the second number

$$\log \left(\frac{x}{y} \right) = \log x - \log y$$

For example,

$$\begin{aligned}\log (5/36) &= \log 5 - \log 36 \\ &= 0.6990 - 1.5563 \\ &= -0.8573\end{aligned}$$

Put into words, the k -value of a *particular mortality factor* is the logarithm (to the base ten) of the ratio of the number of individuals *before* the mortality factor operated to the number of individuals still alive *after* the mortality factor operated. (To help you remember this, take B in N_B to mean *Before* and A in N_A to mean *After*, and use a mnemonic, such as *British Airways* or *Batchelor of Arts*, to get the fraction the right way up.)

In any sequence of mortality factors, for example those that operate on the Wytham Wood owls, each mortality factor has its own k -value.

- ☐ Look at Table 6. How many k -values do you expect there to be for the mortalities that operate over the generation from 24 nesting pairs to nine surviving owlets?
- ☒ Five. This is because there are five mortality factors. Each one operates on the survivors of the preceding episode of death. The k -values for the five mortality factors are termed k_1, k_2, k_3, k_4 and k_5 .

As you would expect, these individual but successive k -values all contribute to *overall* mortality. The term for this overall mortality is **total generation pre-reproductive mortality**, k_{total} . This can also be expressed in logarithmic terms. If N_0 is the initial number of individuals (actual or potential) before any mortality, and N_x is the number after a sequence of x mortality factors, then

$$k_{\text{total}} = \log N_0 - \log N_x = \log \frac{N_0}{N_x}$$

In our owl example (Table 6),

$$k_{\text{total}} = \log N_0 - \log N_5 = \log \frac{N_0}{N_5}$$

If we now take the trouble to calculate the values of each of k_1 to k_5 in this study, and explore the relationship of these with the value of k_{total} , the power and usefulness of this kind of analysis will become clearer.

- ☐ Mortality 1 operates on N_0 to give N_1 . Using the definition of a k -value, calculate k_1 .

■ $k_1 = \log \frac{N_0}{N_1} = \log \frac{72}{51} = \log 1.412 = 0.150$

- ☐ Mortality 2 operates on N_1 to give N_2 . Using the definition of a k -value, calculate k_2 .

■ $k_2 = \log \frac{N_1}{N_2} = \log \frac{51}{43} = 0.074$.

Table 7 is an expanded version of Table 6. The values for k_1 and k_2 have been entered.

TABLE 7 k -values of successive mortalities and generation pre-reproductive mortality (k_{total}) for 24 pairs of owls in Wytham Wood in 1952-3.

Stages	Values of N_0 to N_5	k -values (k_1 to k_5)
maximum total number of eggs if all pairs bred (24×3)	$N_0 = 72$	$k_1 = 0.150$
maximum number of eggs from the 17 pairs that did breed (17×3)	$N_1 = 51$	
actual number of eggs laid	$N_2 = 43$	$k_2 = 0.074$
number of eggs that hatched	$N_3 = 16$	
number of chicks that fledged	$N_4 = 15$	$k_3 = \dots\dots\dots$
number of owlets that survived to form pairs	$N_5 = 9$	$k_4 = \dots\dots\dots$
Potential maximum number of eggs \rightarrow surviving owlets	$N_0 \rightarrow N_5$	$k_{\text{total}} = \dots\dots\dots$

ITQ 6 (a) Calculate the values for k_3 , k_4 and k_5 , and enter them on Table 7.

(b) Calculate k_{total} and enter this on the Table. (Use N_0 and N_5 for the calculation.)

As you can see from the answer to ITQ 6, the sum of the individual k -values for each successive mortality equals k_{total} , the total generation pre-reproductive mortality. That k_{total} can be found simply by adding the individual k -values is one of the strengths of representing mortality in this way*.

- ☐ In our owl example, all the k -values lie between zero and one. Do you think it is possible to have k -values that are greater than one?

■ It is possible and, indeed, very common where mortalities are large. If only ten out of 1000 insects survive a frost, $k = \log \frac{1000}{10} = \log 100 = 2.0$.

- ☐ Is it possible to have a negative value for k ?

■ For $\log N_B/N_A$ to be negative, N_B/N_A would have to be less than one.

* The fact that $k_1 + k_2 + k_3 + \dots + k_x = k_{\text{total}}$ follows from the arithmetical definitions of k -value and k_{total} . You may either accept this, using the worked examples in Table 7 and the answer to ITQ 6 as confirmation, or note the following. $k_1 = \log N_0 - \log N_1$, $k_2 = \log N_1 - \log N_2$, $k_3 = \log N_2 - \log N_3$, $k_4 = \log N_3 - \log N_4$ and $k_5 = \log N_4 - \log N_5$. Therefore, $k_1 + k_2 + k_3 + k_4 + k_5 = \log N_0 - \log N_1 + \log N_1 - \log N_2 + \log N_2 - \log N_3 + \log N_3 - \log N_4 + \log N_4 - \log N_5$. This long sequence simply becomes $k_1 + k_2 + k_3 + k_4 + k_5 = \log N_0 - \log N_5$. The right-hand side of this equation is the definition of k_{total} . Therefore, $k_1 + k_2 + k_3 + k_4 + k_5 = k_{\text{total}}$.

KEY MORTALITY FACTOR

REGULATING MORTALITY FACTOR

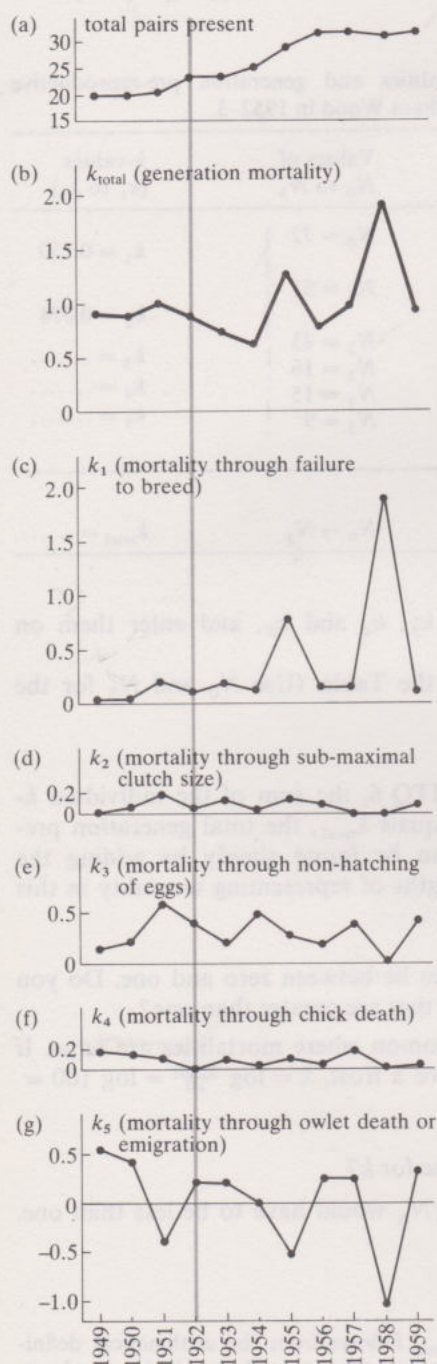


FIGURE 22 k_{total} and k -values for tawny owls in Wytham Wood. (The grey line indicates values taken from Table 7.)

This means that the number after mortality would be greater than the number before the mortality acted. This is not impossible even though it may sound it, because *immigration* at this point in the sequence could occur and thus swell the population.

Besides providing a precise way of representing the sequential deaths that occur in one generation, k -value analysis provides a good way of investigating the change in population from one year to another. Figure 22 shows the variation in each of the k -values, k_1 to k_5 , and in the k_{total} values for each of the 11 years, 1949 to 1959. Its production required, of course, detailed observations for *each* year of the type shown for 1952 in Tables 6 and 7. From an extended study of this kind, various conclusions can be drawn.

- ☐ In which two years were the total generation pre-reproductive mortalities greatest (i.e. in which years was k_{total} very large)?
■ 1958 and 1955 (in that order of size).
- ☐ Which k -value also has high values in these two years (and in what order of size)?
■ k_1 (mortality through failure to breed) in the order 1958 and 1955.
- ☐ Which k -value was particularly low in these two years?
■ k_5 (mortality through owlet death or emigration). In fact, in both years k_5 was negative; there had been a net *immigration* of owlets from neighbouring woods.

These questions and answers have picked out two important features of k -value analysis. The first is that the value of k_1^* varies year by year in the *same* way as k_{total} . In fact, the population at the end of any year is influenced by k_1 (the mortality through failure to breed) more than by any other mortality. In any study of this kind, the mortality factor whose k -values change, year by year, in a pattern that most closely resembles the change in k_{total} , is termed the **key mortality factor**. The second important feature is that the value of k_5 (owlet death or emigration) varies in the *opposite* way to k_{total} , being lowest (in fact, negative) in 1958 when k_{total} was greatest. A factor that varies in the opposite way to the generation mortality tends to alter the numbers away from extremes and towards an average value; its effect is to dampen population change and it is called the **regulating mortality factor**.

You met this concept of population regulation in Section 4.2, where it was noted that mortality factors that regulate populations are *density dependent*: the higher the population density on which the particular mortality acts, the higher is the mortality rate. However, the mathematical relationship between *mortality rate* and *population density* is not linear, and even the curve in Figure 20 is a simplification. This is where k -values which, as we have seen, are mathematical and analytical conveniences, show a real empirical (i.e. experimental) meaning. When a mortality is density dependent, the k -value should be *directly proportional to the logarithm of the population density on which it acts*. Thus when, in Southern's tawny owl study, k_5 is plotted against the logarithm of the number of newly fledged owls, the straight line shown in Figure 23 results.

It is essential that the horizontal axis is the logarithm of the population *on which the mortality in question acts*. Thus, in Figure 23, the horizontal axis must be 'log of number of young fledged' and not 'log of number of eggs laid' or log of any other population in the life-table sequence. Whenever a straight line (or a scatter of points approximating a line) with a positive

* It happens to be k_1 in the owl study. It could be another k -value for some other species. In other words, the key mortality factor is not necessarily the first (earliest) mortality.

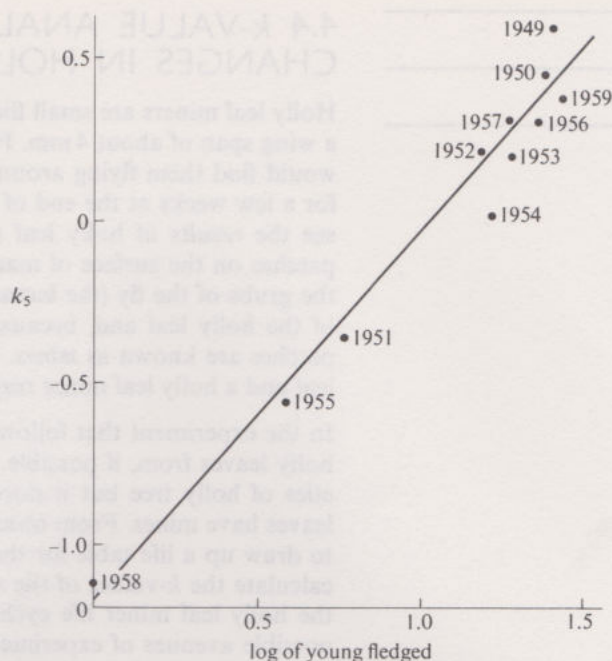


FIGURE 23 Plot of k_5 (owlet death or emigration) against log of the number of young owls fledged.

slope of the type shown in Figure 23 results, then the mortality factor is directly density dependent. All regulating factors are, by definition, density dependent, and it is very probable that k -values giving plots of the type above are regulating factors. However, this should be confirmed by looking to see whether the pattern of annual variation of these k -values is in the opposite direction to that of k_{total} . Most key mortality factors are density independent, but there are some exceptions.

The analysis of k -values has brought us a good way in the investigation of factors that affect owl populations. Even so, the relationship of these factors to tawny owl natural history and to environmental circumstances remains to be discussed. Southern's work was much more extensive in its search for underlying causes than is described here. You saw from Figure 22c that 'mortality through failure to breed' (k_1) is the key mortality factor. But what causes owls to behave—or, rather, fail to behave—in the usual reproductive way? What was it about 1955 and 1958 that was amiss from the point of view of potential tawny owl parents? Southern examined the density of the population of small rodents that form a major part of the diet of owls in spring. He found that at densities of between zero and 15 rodents per hectare there is a very strong inverse correlation between k_1 mortality and rodent density (i.e. as rodent density decreases, k_1 mortality increases, and vice-versa). In 1955 there were only six rodents per hectare and in 1958 fewer than two, compared with as many as 60 in 1959.

An 'answer' to the question posed above—'what causes tawny owls not to breed?'—is, therefore, available in one sense: shortage of spring food. But this is not the final answer. The pursuit of causes and their effects can be taken as far as time, research funding, scientific zeal and/or usefulness to humans permits. What causes the small rodent population to fluctuate: disease, climate, their food supplies ...? How does shortage of spring food alter owl reproductive behaviour? This raises questions about reproductive physiology. None of these questions will be pursued here, though it is important to note these examples of the open-endedness of scientific enquiry and the ever-present link between ecology and physiology. When you study Section 4.5, you will also become aware of the direct importance to human society of population dynamics. But, before then, it will help your understanding of k -value analysis to do the practical investigation described in Section 4.4.

LARVA

PUPA

4.4 *k*-VALUE ANALYSIS OF POPULATION CHANGES IN HOLLY LEAF MINERS

Holly leaf miners are small flies, each with a body of about 1.5 mm long and a wing span of about 4 mm. Few people notice them but, if you looked, you would find them flying around the boughs of many holly bushes and trees for a few weeks at the end of May each year. However, it is much easier to see the *results* of holly leaf miner activity: quite large, rather disfiguring patches on the surface of many of the holly leaves. Such patches are where the grubs of the fly (the *larvae*) have chewed their way through the interior of the holly leaf and, because the grubs feed below the leaf surface, these patches are known as *mines*. Plates 5 and 6 show a typical mine in a holly leaf and a holly leaf miner respectively.

In the experiment that follows, you will be asked to collect 40 or so mined holly leaves from, if possible, one holly tree or bush. There are many varieties of holly tree but it doesn't matter which you choose, so long as the leaves have mines. From observations of the 40 or so mines you will be able to draw up a life table for the holly leaf miner (rather like Table 6), and so calculate the *k*-values of the various mortality factors that operate through the holly leaf miner life cycle (as in Table 7). At that point, various other possible avenues of experimentation will have become apparent, and some of these are mentioned at the end of the Section.

If you were paralleling Southern's Tawny owl work, you would first need to establish the main features of the fly's life cycle, and then find out where, in what sequence and through what agency various mortalities occurred. But is there much mortality?

- ☐ Each female fly lays about 100 eggs (i.e. the fecundity is 100). How many offspring must survive to breed if the population is to remain constant?
- ☒ Two: one egg-laying female and one male. This would ensure that about 100 eggs are laid in the next generation.

So a mortality rate of 98% will result in a constant population for the holly leaf miner; note that for other species the mortality rate that will produce a constant population will be different if the fecundity is different (see Table 8). In general, for non-overlapping generations (i.e. where parents die before their offspring develop), population constancy is achieved if

$$\frac{\text{survival}(\%)}{100} \times \text{mean fecundity} = 2$$

Check that this general statement is correct for one or two other examples as well as for the holly leaf miner using the data given in Table 8.

TABLE 8 Survival and mortality percentages to give population constancy.

Species	Average fecundity	Average survival/%	Average mortality/%
oyster*	100×10^6	2×10^{-6}	$100 - 2 \times 10^{-6} = 99.999998$
fat hen (weed)*	400×10^3	5×10^{-4}	$100 - 5 \times 10^{-4} = 99.9995$
winter moth	200	1	$100 - 1 = 99$
holly leaf miner fly	100	2	$100 - 2 = 98$
mouse	50	4	$100 - 4 = 96$

* For these figures we have assumed that no self-fertilization occurs.

ITQ 7 Using the data in Table 8 for the holly leaf miner, calculate the value of the total generation pre-reproductive mortality, k_{total} . Remember that $k_{\text{total}} = \log(N_B/N_A)$.

But where in the life cycle are the various component mortalities that contribute to this total? The cycle and the mortality factors are summarized in Figure 24. In June, a female fly selects a tender young holly leaf and lays

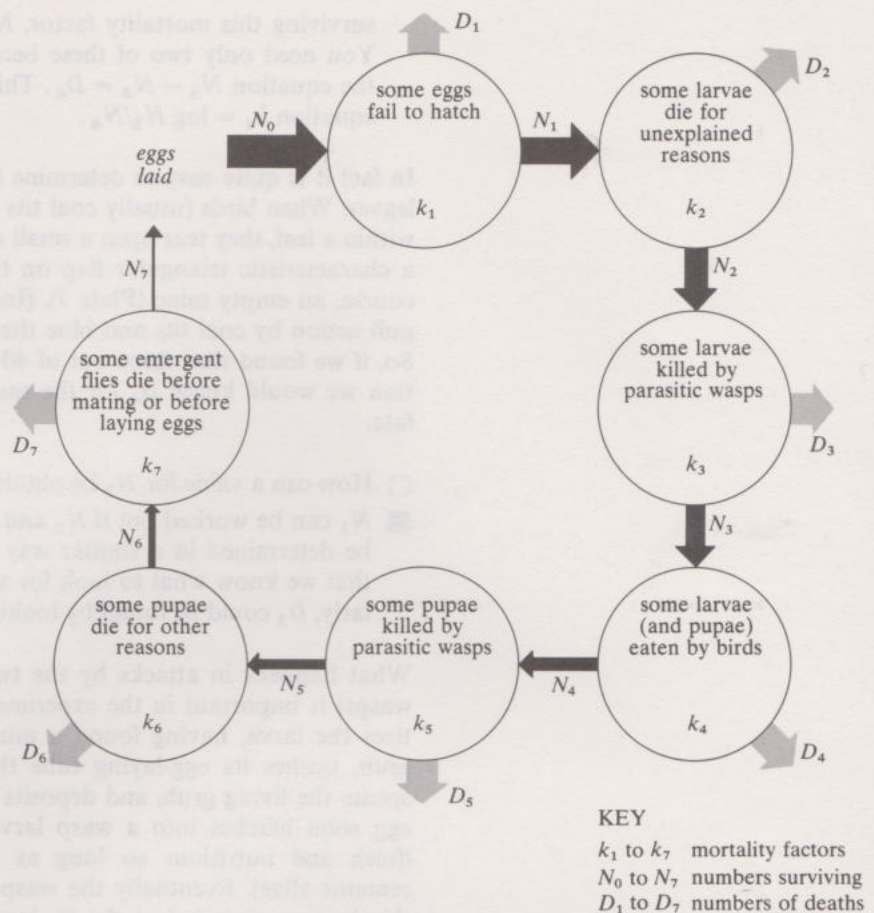


FIGURE 24 Mortality factors acting at different stages of the life cycle of the holly leaf miner.

one (already fertilized) egg inside the midrib of the leaf fairly near the leaf stalk. She goes on to do this to up to 100 or so other leaves. The potential route for each egg is as follows, but remember that most are killed *en route*. The egg hatches quickly into a larva, which tunnels down the midrib towards the centre of the leaf. In September to October the larva, which is by now much larger and hungrier, leaves the midrib and enters the centre part of the leaf blade. Here it eats out a rather large hollow (the mine) in the soft sandwich of tissue lying between the upper and lower surfaces of the leaf. The mine is at its largest by March. Each larva then forms a **pupa** (which is equivalent to the familiar butterfly chrysalis) from which the adult emerges at the end of May, leaving behind the empty pupal case. The emergent fly makes a distinct hole in the leaf surface, usually but not always on the upper side. Adults that successfully emerge may be able to mate, and the cycle begins again when the females lay eggs in the softer tissue of new holly leaves.

As we saw earlier, about 98 out of every 100 eggs fail to complete their development into new adults that mate; even more die in years when the fly population declines, and slightly fewer when the population grows. The main causes of death are summarized in Figure 24. Each of the mortality factors (shown in the circles) has its effect at a particular stage in the life cycle, which means that it is possible to arrange them in a chronological order (although for other organisms the order is less easy to determine). Each of the six inside-the-leaf mortality factors has its own k -value ($k_1 \dots k_6$). Some flies that survive these hazards and emerge as adults fall at the final hurdle and fail to breed; this is the seventh mortality factor, k_7 .

- ☐ Look at Figure 24 and the circle for k_4 , larvae (or pupae) eaten by birds. What information do you need to calculate k_4 ?
- ☒ Any *two* of the following three are sufficient: (a) the number in the population *before* the mortality factor has its effect, N_3 ; (b) the number

surviving this mortality factor, N_4 ; (c) the number eaten by birds, D_4 . You need only two of these because the third can be calculated using the equation $N_3 - N_4 = D_4$. This enables you to calculate k_4 using the equation $k_4 = \log N_3/N_4$.

In fact it is quite easy to determine D_4 by investigating a number of mined leaves. When birds (usually coal tits or blue tits) pick out the fly larva from within a leaf, they tear open a small section of the leaf surface; this results in a characteristic triangular flap on the upper or lower leaf surface and, of course, an empty mine (Plate 7). (Incidentally, this characteristic peck-and-pull action by coal tits and blue tits is also used to open milk-bottle tops!) So, if we found that three out of 40 leaves showed evidence of bird predation we would know D_4 for the sample i.e. that three larvae suffered this fate.

☐ How can a value for N_3 be obtained?

■ N_3 can be worked out if N_2 and D_3 are known ($N_3 = N_2 - D_3$). D_3 can be determined in a similar way to estimating D_4 (provided, of course, that we know what to look for as evidence for parasitized larvae). Similarly, D_5 could be found by looking for evidence of parasitized pupae.

What happens in attacks by the two main kinds of parasitoids (parasitic wasps) is important in the experiment that follows. The wasp that parasitizes the larva, having found a mine containing a living holly leaf miner grub, pushes its egg-laying tube through the layers of leaf cells until it spears the living grub, and deposits one wasp egg within it. The implanted egg soon hatches into a wasp larva, which feeds on the fly larval tissue (fresh and nutritious so long as the progressively consumed fly larva remains alive). Eventually the wasp larva forms a tiny wasp pupa; ideally this happens just before the fly larva dies and begins to decay. The wasp pupa gives rise to a new adult wasp (provided the wasp itself hasn't succumbed to an even smaller parasite!). The adult wasp bores a very small hole in the surface of the leaf, through which it emerges, leaving behind a small, empty, black or dark brown pupal case (Plate 8).

Those fly larvae that survive to form pupae may then be subjected to attack by a range of other species of parasitic wasp. The egg-laying females of these species are able to bore through the outer layers of the holly leaf and the tough outer covering of the fly pupa before depositing the eggs inside the fly pupa where they develop and feed.

☐ What features would you look for in a mine where the fly *larva* had been attacked by a parasitic wasp?

■ If the wasp had emerged successfully there would be a very small exit hole in the surface of the leaf. Inside the mine there would be the very small, empty, black or dark brown case of the wasp pupa. Any remains of the fly larva would have decayed away unless death was recent, in which case there may be remains with fungal growth on them.

☐ What features would you look for in a mine where the fly *pupa* had been attacked by a parasitic wasp?

■ Again there would be a tiny exit hole, provided the adult wasp had successfully emerged. Inside the mine there would be the complete outer covering of the fly pupa (only the material inside this case would be eaten by the developing wasp). In addition, it may be possible to see the

much smaller, empty, wasp pupal case. This is usually black or brown, depending on the species of wasp.

We have now assembled a sufficient list of clues to determine the numbers killed by three mortality factors: bird predation (D_4), larval parasitization by wasps (D_3) and pupal parasitization by wasps (D_5). Two other mortality factors can be identified by observation of the mines: larval death from an unknown cause (D_2), which would leave an empty mine with no clues whatsoever as to what fate had befallen the larva; and pupal death for reasons other than parasitism (D_6), which would leave a brown fly pupal case but no evidence of a wasp pupal case. Note that it is not always possible to distinguish between D_2 and D_3 , or between D_5 and D_6 by observation, however careful. A fly larva or pupa may have been parasitized (D_3) but the wasp itself may have failed to reach the pupal stage, in which case we may misclassify the mine as D_2 from our observations. This may seem an insoluble problem, but provided we check a sufficient number of mined leaves the error introduced by the occasional misclassification will not greatly affect the overall result. This sort of limitation is quite common in biological investigations.

So, we can obtain values for D_2 to D_6 by observation of mined leaves. The two remaining sources of mortality, D_1 and D_7 , cannot be determined by direct observation; we have to rely on indirect means to obtain these data, and these will be described after the experiment.

- ☐ Do observed values for D_2 to D_6 provide sufficient data to calculate each k -value?
- ☒ No, not quite. Each k -value is calculated from $\log(N_B/N_A)$, where the number before and after the factor operated are both known.
- ☐ What further *single item* of information would enable you to calculate all the values of k_2 to k_6 ?
- ☒ Any *one* of N_1 to N_6 will enable you to calculate all the other values. Check Figure 24 again: if any value for N is known, together with each of the D values, you can work forwards or backwards to obtain all remaining N values. For instance, if N_6 could be measured directly you could calculate $N_5 (=N_6 + D_6)$, then $N_4 (=N_5 + D_5)$ and so on. You would then know N_B and N_A for each mortality factor, so you could calculate all the values of k_2 to k_6 .

Fortunately, there is a direct way of determining N_6 , the number of adults that successfully emerge from the leaves. The clue was given earlier: the exit hole of an adult fly is quite different from the exit holes of parasitic wasps. Adult flies emerge through a hole about the size of a pin-head (Plates 9a and b); the hole appears slightly elliptical and has a small triangular hinged flap. If you dissected the mine, you would find a 3–4 mm, empty, brown pupal case with one end hinged open (Plate 9c); the case might contain the thin outer covering (cuticle) of the fly, which was discarded as the fly broke out of the pupa. It is easy to distinguish between a fly emergence hole and a hole caused by emergence of a parasitic wasp because wasp holes are much smaller (the size of a pin-point rather than a pin-head; compare Plates 8 and 9).

In the experiment that follows you will use the approach described above to obtain values for N and D at each stage of the sequence shown in Figure 24. From these data you will be able to calculate each k -value for your sample.

EXPERIMENT

TIME

- 1 Locating a holly bush that is infested with the holly leaf miner and collecting a sample of mined leaves: *time variable*
- 2 Sorting the leaves according to 'cause of death' of the miner grub or pupa: *about 1½ hours*
- 3 Calculating k_2 to k_6 : *30 minutes*

NON-KIT ITEMS

holly leaves
plastic bag and sealing tags
darning needle

KIT ITEMS

Part I
hand lens

ESTIMATING k -VALUES FOR THE HOLLY LEAF MINER, *PHYTOMYZA ILLICIS*

METHOD

LOCATING A HOLLY BUSH AND COLLECTING LEAVES

1 Ideally you should try to find a holly bush in your own locality. For most students this will be fairly straightforward since holly is quite common and widespread in Britain, as indicated on the map in Figure 25. If you live in one of the areas where holly is not so common, you may experience a little difficulty; help should be available at your Study Centre from your tutor or tutor-counsellor, or from other students.



FIGURE 25 The distribution of holly in the UK.

2 Aim to collect a minimum of 40 *mined* leaves from a single bush. You will find that the newer, shiny leaves towards the tip of the branches do not have mines; these are this year's leaves and any grubs inside them have only recently hatched and will still be in the midrib of the leaf. The leaves behind this zone are from last year's growth, and these are the leaves you want; last year's cycle of the miner has been completed, but any evidence of cause of death (or successful emergence) is still present in these leaves.

The boundary between this and last year's growth is usually indicated by a change in colour of the branch: this year's growth may still be greenish whereas last year's growth will be brown. You may also be able to see a circular scar on the branch separating the two zones. This scar marks the point where the bud formed between the two years' growth.

Note that if you go too far back along the branch you will end up collecting leaves that are now two years old. Try to avoid this so that your sample of leaves all come from the same year. The boundary between

EXPERIMENT CONTINUED

these two years is more difficult to see (because there is no change in colour of the branch) but it will also be indicated by a circular scar. Avoid straying into the wrong year if you can—you are trying to obtain valid k -values for one particular year i.e. one generation.

Try to collect mined leaves at random within the correct zone. Avoid the temptation of thinking 'I haven't got a leaf showing bird predation yet—I'll look for one', because this will bias your sample and so make some factors seem more important than they really are. If you are aware that in your sample of 40 leaves there are no examples of, say, successful emergence, then the correct procedure would be to *increase the sample size* rather than to look for a single leaf with this evidence. Unfortunately this approach has implications for your time!

3 Your sample of leaves can be kept in a plastic bag in the chiller (or salad compartment) of a fridge, but *not* in a freezer, until you are ready to continue the experiment. They will last for about six weeks; after this, they may become too brittle for investigating the mines easily.

4 If you wish, you may wash the leaves under a cold tap to remove any bird droppings or dirt before storing them or carrying out the experiment; take care not to damage the leaf surface, which may contain the features that indicate the cause of death of the miner.

SORTING THE LEAVES

Before you start to sort your sample of leaves read carefully through points 1 to 8.

1 The rationale for determining what happened to the fly egg that was laid in each leaf (using a sort of 'biological archaeology') is described in Section 4.4. The indicators of each cause of death are summarized in Figure 26; this chart is also an identification key. You should use this, together with Plates 7 to 9 to determine the probable fate of the occupier of each mine.

2 For each leaf, follow the set of questions and statements in the key to categorize each mine. Some categories are easier to identify than others; for instance, bird predation is very obvious, as is successful fly emergence. With a little practice you will become more confident in categorizing the mines that indicate other fates. Some of these will require you to dissect the mine to look for the pupal case of either the fly or the parasitic wasps (which are much smaller and easy to miss).

3 To dissect the mine, insert a needle close to the exit hole and *gently* peel back the leaf surface to expose the contents; use the hand lens to search for pupal cases. Good lighting (e.g. from a desk lamp) makes the investigation with the hand lens easier.

4 There are bound to be a few leaves in your sample that are difficult to classify. This could happen because there may be other causes of death that haven't been described here, or simply because the evidence isn't complete. If one or more of your samples is impossible to identify through damage or decomposition, discard it. Do not discard casually, just because the 'archaeology' is difficult. When in doubt, do the best you can and then try to make a decision about the category of the mine. If you do have to discard the leaf, record it as 'unknown' and ignore it in your calculations—your sample size will simply be one fewer. There should be no need to discard more than one or two leaves in any sample of 40 leaves.

5 Some leaves may show the following:

(a) *More than one mine on a single leaf* First check that there isn't a thin passageway connecting the two apparently separate mines. If you

EXPERIMENT CONTINUED

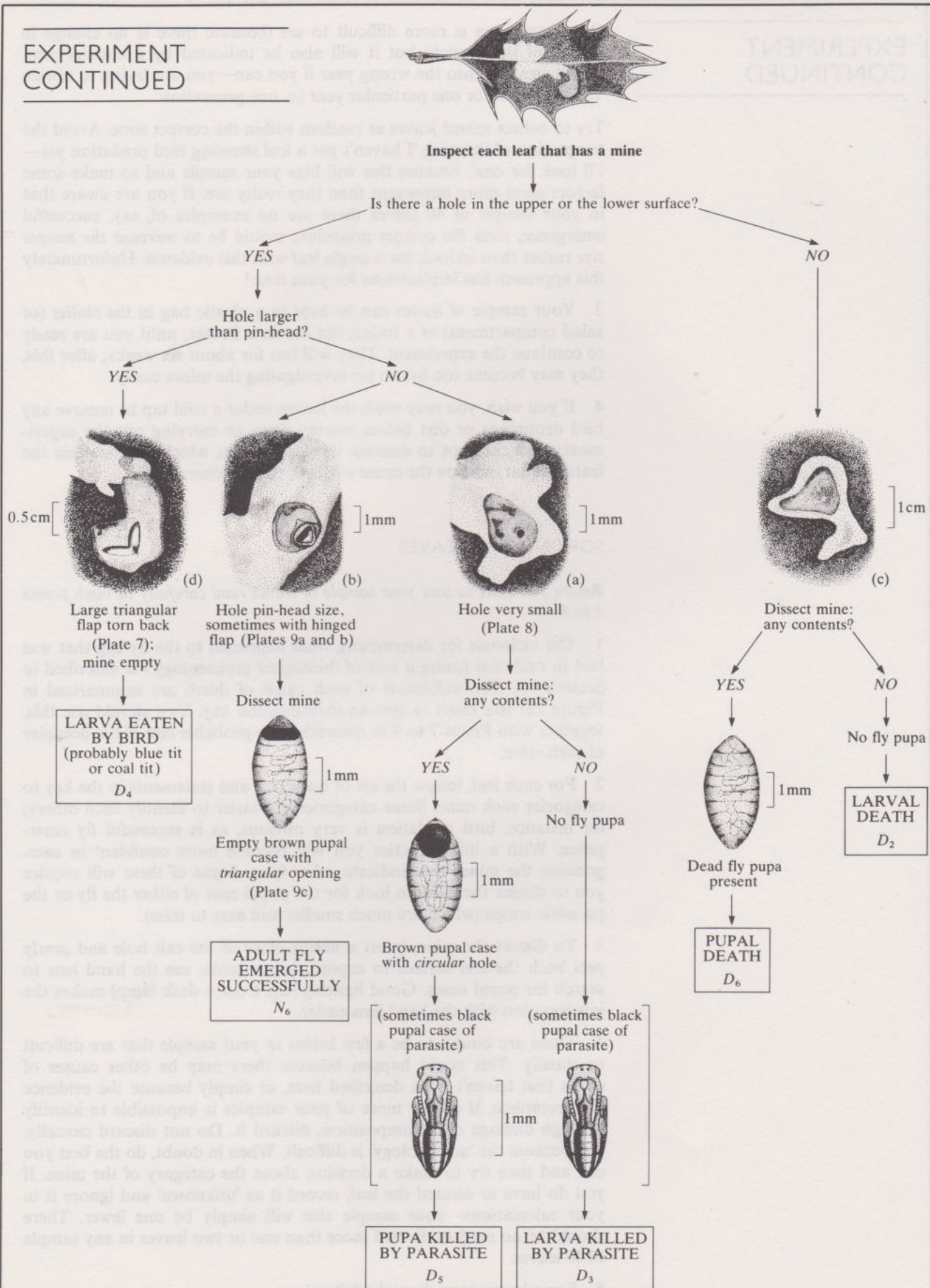


FIGURE 26 Flow chart to use as an identification key for the holly leaf miner experiment.

Some mined holly leaves of different kinds are illustrated: (a) shows a tiny wasp emergence hole, (b) shows a larger fly emergence hole, (c) shows no emergence hole, (d) shows a mine torn open by birds. (Note the mine in (c) is unusually shaped; often it is less convoluted.)

EXPERIMENT CONTINUED

are convinced that two eggs have developed (e.g. you find two fly pupal cases!), then count this as two results and record them both in your Table.

(b) *An empty mine with fungal growth* The fungal growth is often white and hair-like. The most likely fate was death of the larva, so to enable you to distinguish between D_2 and D_3 look *very carefully* with the hand lens for a small black wasp pupal case in the mine (the crucial evidence needed is that which shows whether the parasite survived to pupal stage). The fungal attack could have started on the remains of dead larval tissue, but often the living cells surrounding an old mine become susceptible to fungal attack, so don't assume that presence of fungus automatically identifies the mine as type D_2 or D_3 .

(c) *A series of small holes forming a pattern over the upper and lower surface of the leaf* It might be tempting to classify these as small exit holes of parasitic wasps but, in fact, they're nothing to do with the fly or its parasites. You can see this because they form a regular pattern over any part of the leaf, not just in the area of the mine. These small holes are formed when a mosquito feeds on the very young holly leaf while it is still rolled up; the feeding tube of the mosquito is inserted through the rolled leaf so that when the leaf opens out flat a series of regularly spaced holes appear in the upper and lower leaf surface. An exit hole of a parasite is very different from this: it is a *single* hole on either the upper or the lower surface, and probably has the small, black pupal case of a parasite just beneath it.

6 Emergence holes of the fly and of the parasites are often on the upper leaf surface, but they also appear on the lower surface, so check carefully. When you come across an example of successful emergence, it is worth spending a few minutes investigating the empty fly pupal case. One end of the case will have a hinged lid, which the emerging adult cut away. Inside (or next to) the pupal case you might find the outer covering of the adult insect, which was shed just before emergence. In some cases this covering is almost perfectly intact, giving a good indication of the size and form of the adult fly. A similar shedding occurs when the much smaller parasitic wasps emerge from their pupal cases and you may be able to detect these coverings with your hand lens.

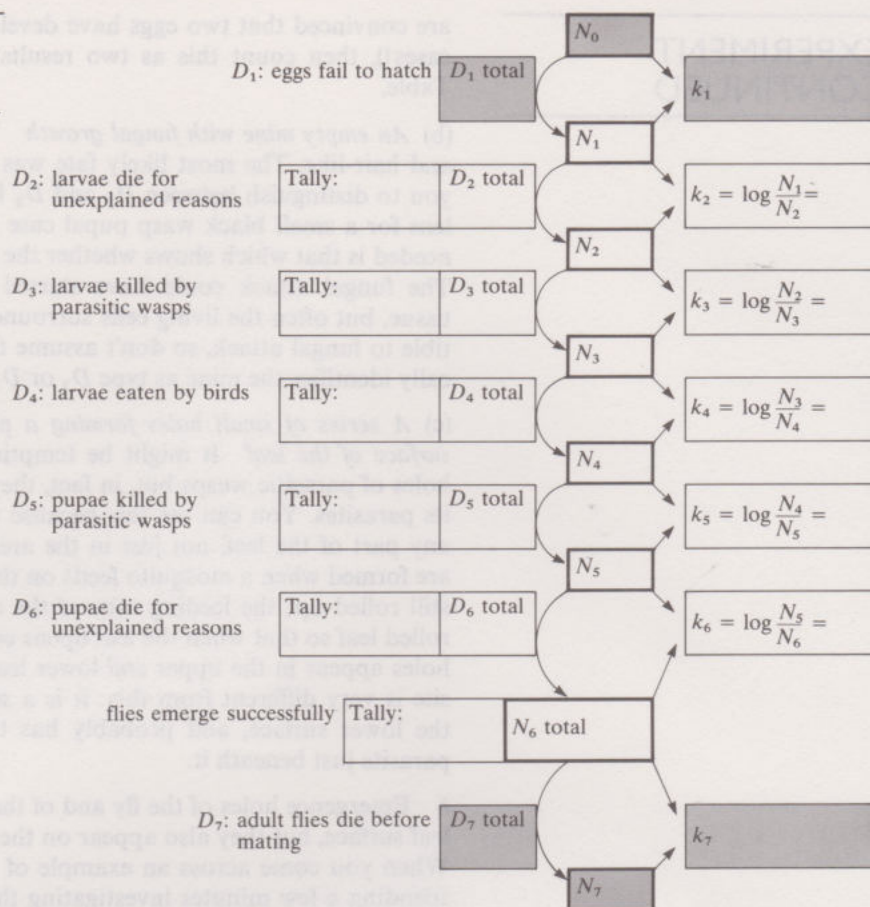
7 Don't worry if your sample of 40 leaves doesn't contain *all* the types shown in Figure 24: there is considerable variation in the pattern of infestation of holly bushes in different parts of the country—even between bushes in the same locality. Your results should be valid for your bush in its particular environment. Remember, any single bush may not exhibit the whole range of mortality factors.

8 Now start to sort your sample of 40 leaves using the information described above and in Figure 26. Keep a tally of the number of mines that fit each category in the key. Use Figure 27 for recording your results. At this stage, just record the number of mines in each category (D_2 to D_6 , and N_6) in the tally boxes (see example in Figure 27). You will use the rest of Figure 27 to help you calculate k -values from these results.

PROCESSING YOUR DATA

1 Using the values you have entered in Figure 27, you are now in a position to calculate each of N_1 to N_5 . (You already have a value for N_6 .) Recall the rationale, given in Section 4.3, for calculating the remaining N values. Note that you cannot work out values for N_0 or N_7 as you have no information about D_1 or D_7 .

2 You can now calculate the values of k_2 to k_6 using the equations in Figure 27.

EXPERIMENT
CONTINUED

Note: you cannot estimate values in the shaded boxes from your observations; indirect ways of obtaining values of k_1 and k_7 are explained at the end of the instructions for the experiment.

Example

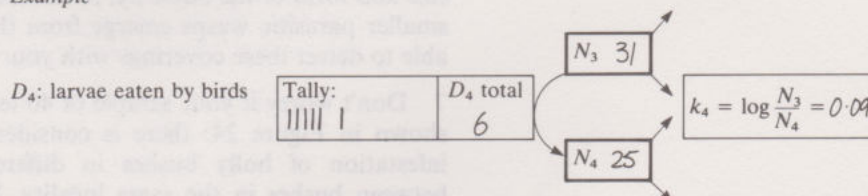


FIGURE 27 Flow chart for recording your results and carrying out k -value analysis for the holly leaf miner.

3 Calculating k_6 . This should be quite straightforward provided you have a value for N_6 ; if you failed to find an example of successful emergence (i.e. $N_6 = 0$), your calculated value of k_6 will be infinity (because $\log N_5/0$ is infinity). This would mean that *everything* that survived to that stage of the life cycle was then killed by that factor. The implication of this is that there would be *no* holly leaf miners in that locality next year—a catastrophic population density decrease! As this has never (or extremely rarely) been observed to happen, if you get this result there is probably something wrong with the method. However, if you looked at *enough* leaves, N_6 would not be zero, hence our advice earlier to increase the sample size, if possible, when this situation arises. (If you cannot do this, for the purposes of this exercise, recalculate k_6 assuming $N_6 = 1$ and D_6 is one less than you observed; this will allow you to calculate a finite value for k_6 .)

4 Estimating values for k_1 and k_7 . These two factors cannot be calculated directly from your data, because you do not have values for N_0 or N_7 . However, you can obtain estimates indirectly by assuming an

EXPERIMENT CONTINUED

'average' value for k_{total} . Recall from the answer to ITQ 7 that if the fecundity of holly leaf miners is 100 and the population is constant, then k_{total} is about 1.7.

- ☐ From this value of k_{total} subtract $(k_2 + k_3 + k_4 + k_5 + k_6)$. What does this number represent?
- ☒ It represents $k_1 + k_7$ because $k_{\text{total}} = k_1 + k_2 + k_3 + k_4 + k_5 + k_6 + k_7$.

Other experiments have shown that survival of eggs within the leaf is normally very high, so k_1 is very small. In fact, k_1 can be safely assumed to be 0, so the value you obtained from the above calculation represents an estimate of k_7 .

Record your values for k_1 and k_7 on Figure 27. You have now found all the 'unknown' values in Figure 27 (and should have completed all the boxes) and obtained k -values for each of the mortality factors that affect the life cycle of the holly leaf miner. You should appreciate that, although this experiment provides a good insight into the holly leaf miner life cycle and the associated k -value analysis, the procedure you have followed does not enable you to identify the key factors or the regulating factors, nor to distinguish between density-dependent and density-independent factors. More data would need to be gathered before the exercise could address these questions (e.g. data over a number of years, to identify regulating factors) and, as you will have discovered for yourself, collecting biological data can be a time-consuming business! Nevertheless, the techniques you have used here provide the basis for such investigations.

The results you have obtained in your experiment may contrast with those obtained by other students, even within your own Study Centre group. These differences could arise either from the different way you obtained your samples or from real differences in the effects of the mortality factors in different locations. Such differences could provide the basis for follow-up experiments (but remember that with group work the labour of data collection can be shared and the sample size increased to avoid some of the problems described earlier). Interesting differences have been observed between adjacent bushes (e.g. when one bush was nearer a street lamp than the other, the levels of bird predation were different), and the level of parasitism has been observed to differ even between north- and south-facing sides of the same bush. We hope you will share your findings with others at your Study Centre and perhaps follow up your initial investigation.

4.5 BIOLOGICAL CONTROL OF PESTS

Fluctuating populations can have great effects on human affairs. Pests have plagued humans for a long time, as the Bible indicates in the Book of Exodus:

... and when it was morning the east wind had brought the locusts.... For they covered the face of the whole land, so that the land was darkened, and they ate all the plants in the land and all the fruits of the trees ... not a green thing remained, neither tree nor plant of the field, through all the land of Egypt.

There are several chemical methods of controlling pests. One way is to use the blunt-ended bludgeon of wide-spectrum (i.e. not very selective) insecticide sprays. A more selective approach is to use insecticides that are taken up into the plant sap ('systemic' insecticides) and kill only the herbivores that consume the plants. But the most specific approach is to use pheromones as described in Units 17–18. The commonly used insecticidal

BIOLOGICAL CONTROL

methods give quick and reasonably certain relief to the hard-pressed agriculturist. But increasingly they are giving cause for concern over pollution (insecticides often do not degrade readily), cost (they are expensive and need to be applied frequently) and long-term unreliability (pest populations may evolve resistance to a pesticide).

Biological control usually involves the deliberate introduction of an organism (whether a bacterium, a virus or an insect) that is a predator or parasite of the pest. The chief problems are that time is required to research and introduce biological control agents, and that there is no guarantee of success. Of 223 attempts at biological control up to 1969, only 42 achieved complete success—and a few went very wrong when a predator that was introduced to attack a pest attacked some other prey instead. Such problems are real enough to farmers who see their crops being consumed before their eyes: often they see insecticides as the solution.

The first pest controlled biologically was the cottony cushion scale insect, *Icerya purchasi* (Plate 10). When the Californian citrus fruit industry was established in the early 1850s, orange, lemon and lime trees were imported from Australia. The citrus trees came with their scale insect pest but, unfortunately, without the natural enemies of that insect. The scale insects rapidly invaded the citrus trees, and their population burgeoned. Debilitating the trees by sucking their sap and covering the leaves with scale excretion that hosted parasitic fungi, the pests threatened the whole citrus fruit industry with collapse. A biologist went from California to a region of Australia where the scale insect was not a pest of local citrus trees to look for natural enemies. He returned with two species that attacked *Icerya* in Australia, and one of these—the ladybird beetle, *Rodolia cardinalis*—proved to be a most effective agent of biological control. In 1889, 500 of these beetles were released in California. They spread rapidly and the scale population was reduced to negligible proportions. A telling postscript to this story of successful biological control was provided in the late 1940s when the chlorinated hydrocarbon insecticide DDT was used against other pests in California. An unexpected outcome was the re-emergence of cottony cushion scale as a pest. It soon became apparent that *Rodolia* was more susceptible to DDT than *Icerya*, and the decrease in predator population led to an upsurge in its prey, the citrus-destroying scale insect.

In all examples of biological control there is a fine balance between the population of the pest and that of its predator or parasite. If a prey population increases, a little later the predator population will increase too; the increased predator population will lead, after a short while, to a fall in the prey population. Figure 28 shows this relationship in another example of successful biological control: the control of whitefly, *Trialeurodes vaporariorum*, a pest of greenhouse cucumbers, by the minute parasitic wasp, *Encarsia formosa*. The 'lag' between peaks is a typical result of predator/prey and parasite/prey interdependence.

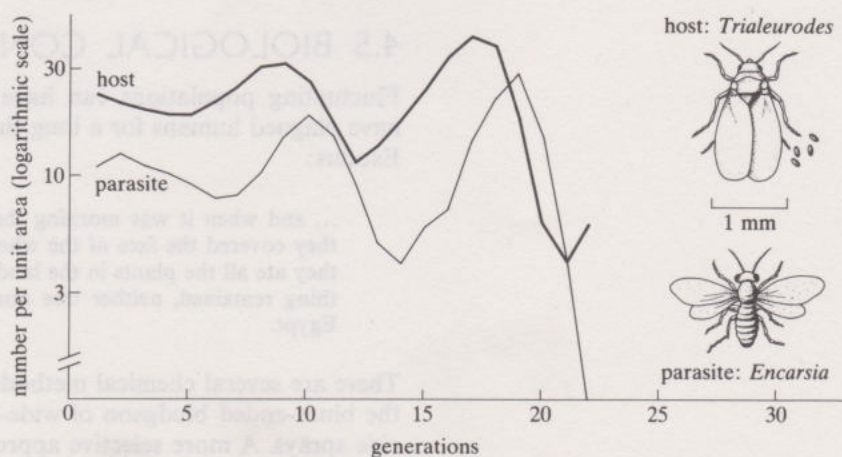


FIGURE 28 The interaction between the greenhouse white-fly, *Trialeurodes vaporariorum*, and its wasp parasite, *Encarsia formosa*, over twenty-two generations. Note the log scale.

The examples of biological control described above both depend on (a) the mortality of the *pest* by predator attack increasing as the *pest* population rises, and (b) the mortality of the *predator* by starvation increasing as the *predator* population rises. These are both examples of density-dependent mortality, and closer analysis would show that (a) is the regulating mortality factor for the pest and (b) is the regulating mortality factor for the predator.

A rather different kind of biological control depends on mortality through reduced fecundity. Control of the screw-worm (which lays eggs in the hides of cattle and frequently kills them, and is prevalent in the southern USA) is an excellent example. The female mates once with a male and takes into herself a supply of sperm, which she uses to fertilize her eggs throughout her egg-laying life. Control is effected by releasing before the start of the fly breeding season millions of screw-worm pupae that have been factory-produced and *sterilized by radiation*. When these pupae hatch, the sterile males mate with females from the wild population giving, of course, a totally barren union. (The impact of sterile females is not significant.) Some eggs are fertilized by males from the wild population males, but because the wild population is 'diluted' by the sterile interlopers, the screw-worm fly population is massively reduced. This method of control is very expensive but, in particular instances, highly effective and worthwhile.

SUMMARY OF SECTION 4

- 1 *Population ecology* is about how changes in births, deaths, immigration and emigration alter or maintain the size of a population.
- 2 The number of births and deaths in a population may be affected by the number of predators (or parasitoids) of a higher trophic level, and by the availability of food in the trophic level beneath.
- 3 *Mortality rate* and *natality rate* are defined as the proportion or percentage of the population that has died or been born, respectively. These rates frequently change with the density of the population and have a regulatory effect on its size.
- 4 The impact of the mortality factors that affect the survival of the members of a population may be calculated from a *life table*. The numbers in a life table can also be used to plot a *survivorship curve*.
- 5 *k-value* analysis uses life tables gathered over a number of years for a population to calculate the effect of different mortality factors upon fluctuations in population size. The factor whose pattern of annual variation in *k-value* most closely parallels that of the annual variation of total generation mortality, k_{total} , is called the *key mortality factor*. *k-value* analysis also detects density-dependent mortality factors. *Regulating mortality factors* are always density dependant.
- 6 The natural enemies of pests can be used as agents of biological control to reduce pest numbers to acceptable levels.

SAQ 10 Is each of the following statements *true* or *false*?

- (a) If a population is to be stable, the pre-reproductive mortality in any generation must equal the fecundity of the parent generation.
- (b) Life tables and survivorship curves always show a large mortality early in life.
- (c) Key factors are always density dependent.
- (d) *k-values* typically remain the same every year.
- (e) Regulating factors are always density dependent.
- (f) The biological control of pests is always more efficient than chemical control.
- (g) A mortality factor is density dependent if it accounts for a constant number of deaths each year.

ZONATION

SAQ 11 (This is intended for extra practice in handling data.) The following data are for the winter moth in Wytham Wood. They show the average number of individuals killed by each of six sequential mortality factors.

number of eggs laid by female moth	200
number of caterpillars killed by 'winter disappearance'	184
number of caterpillars killed by the parasitic fly, <i>Cyzenis</i>	1
number of caterpillars killed by other parasites	1.5
number of caterpillars killed by disease	2.5
number of pupae killed by predators in the soil	8.5
number of pupae killed by the parasitic wasp, <i>Cratichneumon</i>	0.5
number of adults surviving to breed	2

(a) Convert these data to show the average numbers of individuals surviving after each mortality.

(b) Convert the average numbers surviving into a life table, starting with 100 eggs.

SAQ 12 (This is intended for extra practice in calculating k -values.) From the numbers of winter moths surviving at each stage (calculated in answer to SAQ 11a), calculate the values of

- k_{total} , the total generation pre-reproductive mortality,
- k_1 , the mortality due to 'winter disappearance',
- k_2 , the mortality due to parasitism by the fly, *Cyzenis*,
- k_3 , the mortality due to other parasites,
- k_4 , the mortality due to disease,
- k_5 , the mortality due to predators taking pupae in the soil, and
- k_6 , the mortality due to parasitism by the wasp, *Cratichneumon*.

SAQ 13 Some data for the cinnabar moth were analysed by counting the numbers of larvae that died from each of several causes. Three main mortality factors, which acted sequentially, were identified: k_M , the mortality due to mites and other animals eating the very young caterpillars; k_S , the mortality due to starvation because the caterpillars had defoliated the ragwort plant; k_A , the mortality due to parasitism by a wasp, *Apanteles*.

(a) Figure 29 shows the values for k_{total} , k_M , k_S and k_A plotted for the years 1966 to 1973. Can you identify a possible key mortality factor?

(b) Can you identify a possible regulating mortality factor? Is this cinnabar moth population subject to strong regulation (as are tawny owls) or weak regulation?

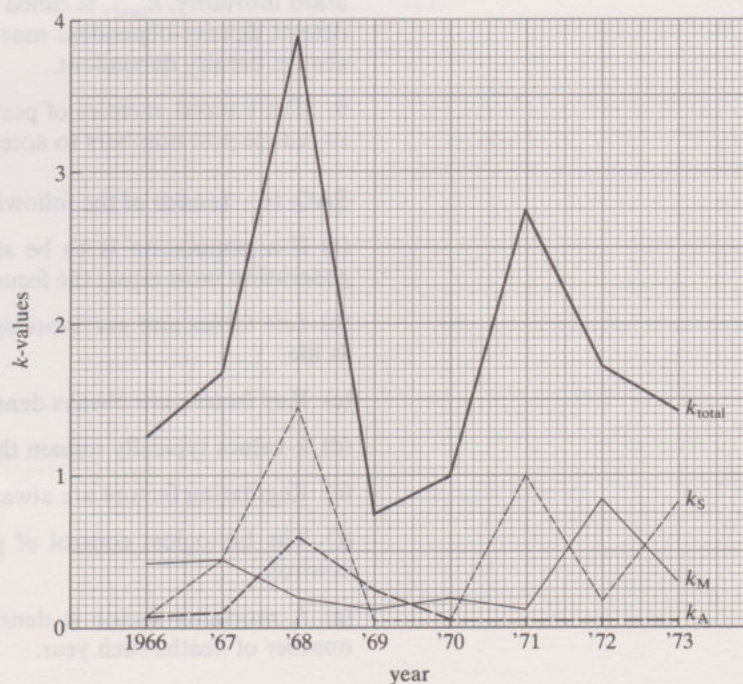


FIGURE 29 k_{total} and k -values for the cinnabar moth.

5 ECOLOGY OF COMMUNITIES

There is a story about an ecologist who was director of a field station on the River Stour in Essex. The students who visit this field station are told that they should not collect any plants from the habitats in the surrounding area, but one day the director found a heap of plant specimens which a wayward student had collected and then thrown away. After dinner that evening the director stood up and said: 'I want to see in my study the person who this afternoon walked along the river as far as the bridge, then walked across the middle of the salt marsh and returned to the Field Station, via the edge of the oak wood and across the bottom of the meadow.' Not long afterwards the culprit who had collected the plants turned up at the director's study, convinced that the director had supernatural powers. Of course the director was really just using his knowledge of plant communities and where different communities were to be found in the vicinity of the field station to work out what route the student must have taken to collect those particular plant species. The study of communities and what species are to be found in them is a specialized branch of ecology, which we shall look at in some more detail in this Section.

5.1 NICHES

In Section 1 we defined a *community* as a group of species that live in the same habitat. Let us take a particular community and think further about the situation these organisms find themselves in. Figure 30 shows the distribution of a community of algae and invertebrate animals typical of rocky seashores on the west coast of the British Isles.

- ☐ *Chthamalus stellatus* and *Balanus balanoides* are two species of barnacle. How are they distributed relative to each other in this habitat?
- ☒ *Chthamalus stellatus* occurs in a band at the top of the shore and *Balanus balanoides* occurs in a band below it.
- ☐ Is the banded distribution shown by the two barnacle species typical of the organisms in this habitat, or are the other species jumbled up together?
- ☒ All of the species in the diagram show a banded type of distribution, so the barnacles are typical of this community in this respect.

This banding pattern is called **zonation**. You may ask why the plants and animals occur in bands like this. The brief answer is that there is a *gradient* in the physical environment down the shore, and species respond differently to this.

- ☐ How is the physical environment likely to vary between high water mark and low water mark?
- ☒ Physical disturbance from waves and the period of exposure to the air will vary between high and low water marks.

The gradient in these physical factors can explain some of the zonation in the distribution of species. For example *Chthamalus* is more resistant to desiccation than *Balanus*, which is why it can occur higher up the shore. But biotic factors are responsible for the pattern too. The upper distribution limit of *Balanus* might be determined by the hazard of desiccation high up the shore, but what determines the lower limit of the *Chthamalus* band? Although as adults barnacles are stuck to the rock, as tiny free-floating larvae they are washed to-and-fro across the entire shore by the tides. So it is reasonable to ask why adult *Chthamalus* don't occur lower down. In one of the classic experiments of ecology, J. H. Connell tested the idea that competition between *Chthamalus* and *Balanus* is responsible for the lower distribution limit of *Chthamalus*. He simply removed *Balanus* from parts of the shore and returned to find out what happened some time later. He found that *Chthamalus* now lived in the top part of the *Balanus* zone, where the latter had been removed.

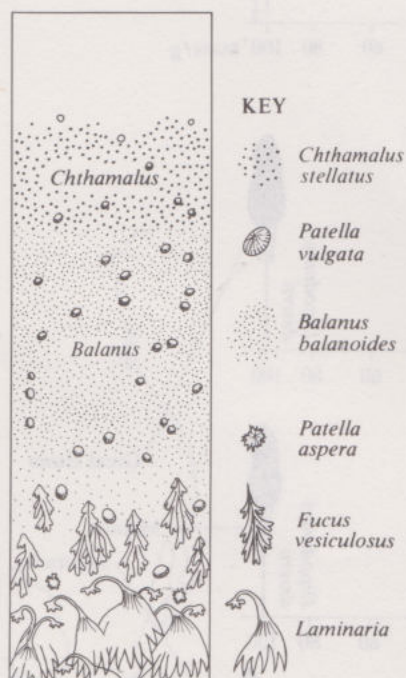


FIGURE 30 The distribution of *Chthamalus* and *Balanus* barnacles on a semi-exposed shore. *Chthamalus* is able to survive on the drier upper shore but *Balanus* is restricted to a zone nearer the sea. *Fucus vesiculosus* and *Laminaria* are seaweeds; *Patella vulgata* and *P. aspera* are limpets.

NICHE

FUNDAMENTAL NICHE

REALIZED NICHE

Many biotic factors vary in parallel with the physical gradient, thus reinforcing its effect upon the distribution of animals and plants found there.

- ☐ Can you think of how the physical gradient down the shore might cause parallel differences in the activity of predators that feed upon shore animals?
- ☒ Many shore birds search for food behind the retreating tide. The higher reaches of the shore are more dangerous for the animals on which they feed because these areas are exposed for a longer period each day. Conversely, animals in these areas will be less vulnerable to marine predators. For example, the dogwhelk, *Nucella lapillus*, which feeds on barnacles, can spend more time feeding on the lower shore than on the upper.
- ☐ How would you test the hypothesis that the position of the lower limit of the *Balanus* zone is determined by predation on the barnacles by *Nucella lapillus*?
- ☒ You would need to remove the dog whelks from some parts of this zone and compare the lower limit of barnacles there some time later with control areas from which dog whelks had not been removed.

Rocky sea shores are unusual environments in that physical conditions vary in a predictable way, which causes a clear pattern of zonation among the species present. Although it is always more difficult to see, organisms found in other habitats appear to divide resources between them along gradients in physical and biotic conditions in a similar way to rocky shore dwellers. For example, look at Figure 31 and then try the following questions.

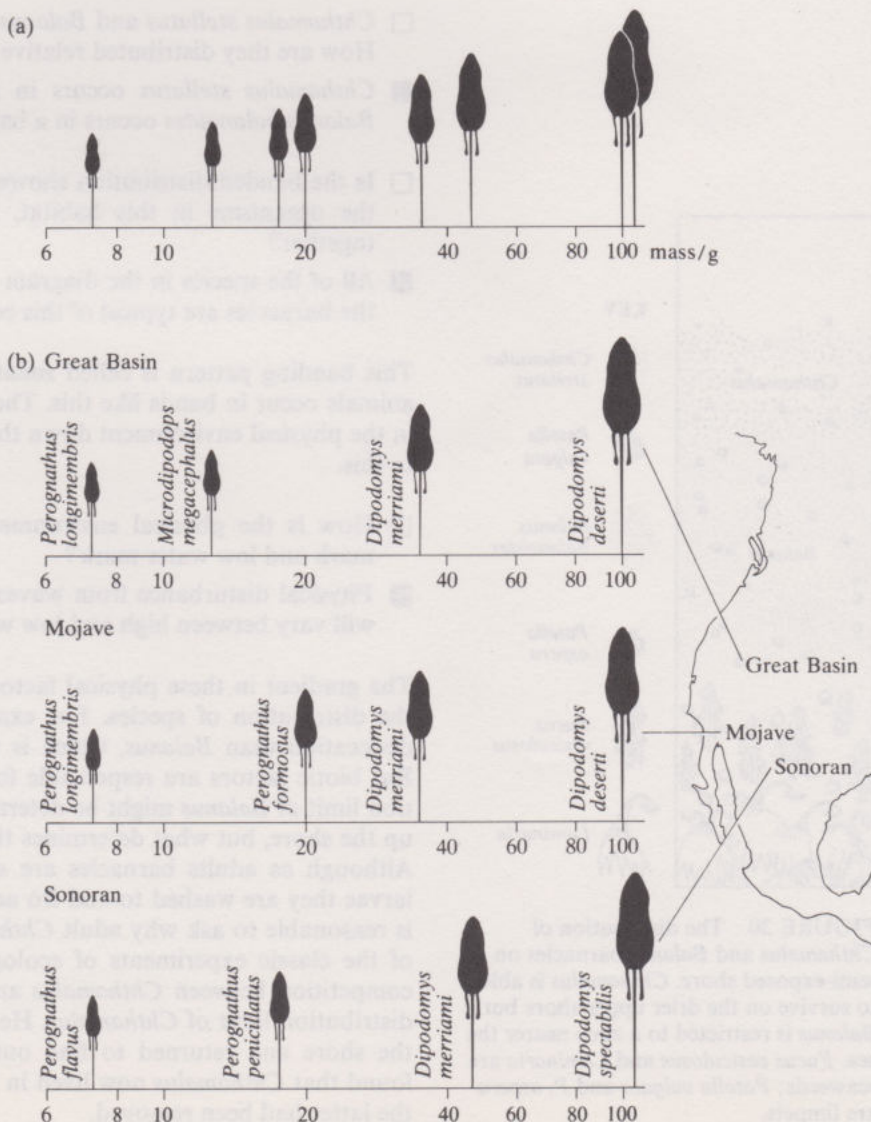


FIGURE 31 Eight species of seed-eating rodents occurring at three sites in the deserts of S.W. North America. The average adult mass of the species varied between 7 g for *Perognathus longimembris* to more than 100 g for *Dipodomys spectabilis*. The average body masses for all eight species are shown on a scale at the top of the diagram (a). Four species occurred at each of individual desert sites as shown in (b).

- ☐ Pick any four *adjacent* species of seed-eating rodents from the eight shown in Figure 31a, and write down the range of body masses. Then look at the four species of seed-eating rodents found at the site in the Great Basin Desert whose body masses are shown in Figure 31b. How does their range of body masses compare with the four species from 31a? Repeat the comparison for the Mojave and Sonoran Deserts. Is the range of body masses of species living in the same desert smaller or greater than you would expect from the range of body masses in your chosen sample from Figure 31a?
- The range of body masses found in each desert is always greater than that for any four adjacent species in Figure 31a. One explanation for this is that the ecology of seed-eating rodent species is related to their body size and, therefore, differences in body size reflect differences in the species' use of resources.
- ☐ If body size is related to the kind of seed a rodent collects, why might you expect the seed-eating rodent species living in the same habitat to have different body sizes?
- Because similar sized species would compete for the same seeds, perhaps causing one of the competitors to be displaced from the habitat altogether. The ecological significance of body size is not fully understood in these rodents, but experiments have established that species of similar size do compete with each other.

The term ecologists give to a barnacle's bit of the shore, a rodent's share of seed resources or any species' share of its habitat is its **niche**. The part of the habitat that a species can use in the absence of competitors and predators is called its **fundamental niche**. The part that it actually uses, when competitors and predators are present, is called its **realized niche**. The only way we can find the full extent of a species' fundamental niche is by experimentally removing predators and/or competitors as Connell did on the rocky shore.

The seashore gives a misleading impression that niches are easy to identify. In practice, the niche can be an elusive concept and this has led some ecologists to question the usefulness of the idea. Nevertheless, it is a term that clearly does have a use when we are trying to describe a particular set of physical and biotic conditions in a habitat where we find, by experience or by experiment, that particular species occur.

5.2 CHANGES IN COMMUNITIES WITH TIME

Ecological communities are not static collections of species, frozen in space or time; as a rule they change.

- ☐ What examples of community change have you already come across in Unit 25?
- Spraying insecticides in banana plantations causes changes in the insect community. Migratory movements and irruptions of birds may cause changes in the communities to which they move.

The most obvious changes to communities are those caused by human activities, but natural changes are also important. Some of these operate on a grand scale and require an historical perspective for us to appreciate them. Plant communities in Britain today are composed of species that have been able to recolonize these islands since the last glaciation, about 13 000 years ago. Norway spruce, *Picea abies*, is a very common tree on the European continent. It is quite able to grow in our climate, (as proved by the Forestry Commission's plantations), and is probably only missing from the native flora of Britain for historical reasons. Those species of native tree that recolonized the British Isles first have the highest number of insect species associated with them, suggesting that these insect communities may have accumulated species with time. New insects are still arriving in Britain, a notable recent arrival being the tiny gall wasp, *Andricus quercus-calicis*, which attacks oaks and causes them to produce the Knoppe gall.

CYCLICAL REGENERATION

SUCCESSION

CLIMAX COMMUNITY

There is a change in the composition of virtually all plant communities after the death of major components of the vegetation. The fall of large trees, such as mature oaks, in forests allows light to penetrate to the forest floor where young trees of fast-growing, short-lived species, such as birch, take their place. Short-lived species are eventually replaced in their turn by the slow-growing species. Consequently, natural forests are often made up of a mosaic of patches representing the different stages of this **cyclical regeneration**.

If new ground becomes available a **succession** of plants and animals will colonize the area. First to arrive in a newly abandoned arable field will be the short-lived plants, such as annual meadow grass, which often has a high density of seeds in the soil. With time, long-lived plants replace the short-lived ones; birds deposit the seeds of shrubs such as hawthorn in their droppings and after a while trees with large seeds, such as acorns, dropped by squirrels or jays, may arrive. Ultimately, an abandoned field in Britain is likely to end up as an oak wood, and so this type of woodland has been called the **climax community** of Britain.

☐ Do climax plant communities ever change?

■ Yes. As we described, a process of *cyclical regeneration* occurs in such woodlands.

Grazing animals are an important agent of change in plant communities, and they may prevent the succession of vegetation, which would normally lead to woodland, from taking place. The history of the rabbit in Britain amply illustrates how far-reaching a grazer's effects can be. In Section 5.3 and TV 25 we consider this in some detail.

5.3 RABBITS AND VEGETATION (TV PROGRAMME)

The rabbit, *Oryctolagus cuniculus*, is a native of Europe that has been carried to many parts of the world because it is good to eat and has useful fur. It breeds readily in captivity and is fairly hardy, being able to survive in central Africa as well as in the harsh climate of Tierra del Fuego (just North of Cape Horn). Rabbits were probably introduced into Britain during Norman times; their close relatives, the hares, are native British species.

In medieval times, rabbits were reared in warrens as a source of food for feasts and for their fur. Some escaped, and wild populations became established and spread, especially after it became common practice to reduce numbers of predators in order to protect game birds. In 1948, the annual catch of wild rabbits in England and Wales was estimated to be between 60 and 100 million animals.

Meanwhile, as shown in TV 25, rabbits had been introduced into Australia; they multiplied there and spread through two-thirds of the continent. Trapped rabbits supported an export trade, based on meat supplied to Britain and fur to the USA, worth several millions of pounds annually; but rabbits were clearly pests. They caused deterioration of pastures on a very large scale. Attempts to introduce the viral disease myxomatosis from South America, as a form of biological control, started in 1936 and were eventually successful in 1950, when mosquitos acted as carriers transmitting the virus from sick rabbits to healthy ones.

About a million square miles were infected in the summer of 1950–51 and there were further epidemics in the following summers, with 1952–3 as the peak year. Mortality among infected rabbits was 99.5% to start with, but fell to less than 90% by 1955, probably as a result of a change in the virus and the appearance of resistance in young rabbits. There were dramatic effects on sheep production: the increase in wool production alone was worth some £34 million; other increases in rural production brought the total profit to £50 million.

Myxomatosis was introduced into France deliberately in 1952 and spread rapidly, reaching almost every part of the country by 1953. It also spread to the Netherlands, Kent and Sussex in the summer of 1953. The method of introduction is not known, but it was not a deliberate act by anyone in authority. By the end of 1954, the disease had spread almost throughout this country. In Britain, the carrier is the rabbit flea, which breeds in burrows where the female rabbits bear and suckle their young. Some rabbits do not make burrows and nests, and these are much less likely to contract myxomatosis.

Let us now consider the effects in Britain of the disappearance of almost the whole rabbit population through myxomatosis. As shown in TV 25, rabbits are grazing herbivores; not surprisingly, the areas where their disappearance made the greatest impact on the vegetation were the chalk downlands, which are characteristic of southern England. In the middle Ages, these were grazed by sheep but in more recent times the principal grazers have been rabbits.

- ☐ Would you expect the plant community of the chalk downlands grazed by rabbits to be a climax community?
- No. As grazing could prevent the establishment of tall plants, the community is not likely to reach the climax stage.

Two such chalky areas are shown in Plates 11 and 12, which are photographs, taken in spring and summer, of Lullington Heath in Sussex and Old Winchester Hill in Hampshire, respectively. The first photograph in each pair (11a and 12a) were taken in 1954 before myxomatosis reached the area, and the second ones (11b and 12b) were taken after almost all the rabbits in each locality had been killed by the disease. This was in 1967 for Lullington Heath and in 1956 for Old Winchester Hill.

At Lullington Heath, there is an obvious change in vegetation from broken turf with bare chalk and a few bushes in 1954, to a dense sward of grass with a tangle of brambles in 1967. The rabbit burrows in 1954 were surrounded by areas of bare chalk with some patches of turf. The bushes near the burrows are elder, *Sambucus nigra*; these plants are unpalatable to rabbits. In contrast, red fescue grass, *Festuca rubra*, formed a closed community in 1967 with bramble bushes, *Rubus* species. Thus, a new plant community has grown on Lullington Heath following the death of the rabbits.

The elimination of rabbits had an equally visible but somewhat different effect on the community of Old Winchester Hill. This change occurred over just two years.

- ☐ What is the obvious change over this period? Compare Plates 12a and 12b.
- The tall yellow flowers present in 1954 are absent in 1956. A closer inspection than the photograph allows would also show that patches of chalk scree in 1954 have been colonized by grasses by 1956.

The tall yellow flowers are ragwort, *Senecio jacobaea*, which, like elder, is unpalatable to rabbits. Each ragwort plant lives for only two years, and most grow from seed. These seeds were able to establish themselves on exposed chalk where the ground was scratched by rabbits. After myxomatosis, plants of other species grew over the bare chalk, and ragwort seeds failed to establish themselves in the face of this competition.

The plants of the chalk downland of 50 years ago usually formed a community with leaves close to the ground, and often they had attractive flowers (for example, thyme). Absence of grazing allowed faster growing shrubs and herbs with leaves further from the ground to spring up and overshadow the traditional downland plants. The conservation of the original, attractive community requires active management; people now work to clear the scrub of brambles and hawthorn, or maintain flocks of sheep to graze chalk grassland nature reserves.

Plates 13a to 13g and 14a to 14g, illustrate points discussed in TV 25, and include photographs of chalk plants and of plants associated with rabbits. Biologists had realized before 1954 that the activity of rabbits was important in determining the composition of certain plant communities. When small areas of land were enclosed with rabbit-proof netting, plants appeared that did not grow outside. But the almost complete disappearance of rabbits led to much greater changes in vegetation than most biologists expected.

In addition to changes in vegetation, there were, as you might expect, some changes in animal populations, especially of those species that ate rabbits or competed with them for food. Hare populations increased steadily after the rabbits disappeared. Foxes and other carnivores switched their diets to take larger numbers of voles and mice; some lowland foxes probably also took increased numbers of poultry and game birds. There was no evidence that foxes suffered any mortality, or even lost much weight, when they lost an important component in their diet; they were sufficiently versatile to exploit other food sources.

As these observations show, the elimination of rabbits by myxomatosis alters a major part of the structure of the community and, in so doing, has far-reaching and often unpredicted effects. This is shown even more powerfully in TV 25 when rabbits were introduced to a country previously without them: only by bringing to bear the rabbit-eliminating power of myxomatosis (in a very successful example of biological control) was it possible for Australian farmers to turn the tide on the great rabbit plague.

SUMMARY OF SECTION 5

1 The banded distribution pattern typical of organisms found upon rocky sea shores is called *zonation*. Zonation reflects the gradient in the physical conditions of the environment between tide marks, and the effects of this gradient on ecological processes such as predation and competition.

2 The occupation of different zones of the environment by different sea-shore organisms is the clearest example of species having their own *niches*. The fundamental niche is that part of the habitat that a species may potentially use when its predators and competing species are absent. The realized niche is the part of the habitat used when predators and competitors are present. A species' fundamental niche can only be determined by experimentally removing predators and competitors.

3 Changes in communities are the rule rather than the exception. Human influence has the most dramatic effects, but there are also natural processes of *cyclical regeneration* and *succession* in most communities. Without human intervention, vegetational succession leads to a *climax community*. Cyclical regeneration occurs in climax vegetation too.

4 Grazing animals are responsible for major effects upon vegetation and plant communities. The effect of rabbits on British and Australian vegetation was demonstrated quite dramatically when these animals were suddenly eliminated by myxomatosis.

SAQ 14 For each of (a) to (e), decide whether the statement is true or false.

- The realized niche of a species can be described from observation alone and need not be tested by experimental removal of other species.
- The fundamental niche of a species can be described from observation alone and need not be tested by experimental removal of other species.
- Competition between species may exclude a species from a part of its fundamental niche.
- The species composition of a community, such as that found in a rocky shore habitat, is the same wherever the habitat is found.

- (e) Major changes in communities are caused only by human activities.
- (f) Climax communities, by definition, do not change their composition.

6 ECOLOGY IN CONTEXT

This Unit has shown how organisms in a community interact with one another; how they affect and are affected by each other's energy and chemical needs; how their numbers impinge upon one another; and how they depend upon the physico-chemical features of their environment, which they, in turn, each influence. Two major messages of this Unit are that the relationships among organisms living within a community are intricate, and that they are very sensitive to the precise conditions of their environment.

In view of this intricacy and sensitivity, the third major message is not surprising. This is that humans have a great and immeasurable capacity for influencing the balance of each and every ecosystem; this has been explored at many points in this Unit. Many of our present problems as a species arise from a rapidly growing population requiring food, hospitable territory and protection from disease. In finding solutions to these problems, our influence on ecosystems is increasingly baleful. This Unit has touched upon problems of atmospheric carbon dioxide levels, eutrophication and nitrate toxicity, acid rain pollution and soil erosion from tree-felling. Other kinds of pollution, notably those caused by radioactive wastes and heavy metal poisons, have not been discussed. However, by considering energy relationships, mineral and biogeochemical cycles, and the interaction of populations in the framework of ecology as a science, we have provided the basis for making an informed assessment of these wider societal aspects of ecology.

But it is with ecology as a part of the science of biology that we close. We have been brought back full circle to the beginning of our study of biology in Unit 19, where we noted how exquisitely well-adapted many organisms appeared to be to their environment. We now see that adaptation does not simply consist of being well camouflaged as a defence against predators, or being able to run fast to catch prey, although these certainly are important adaptations. Adaptation ranges far wider. It embraces an organism's ability to survive and reproduce successfully in an environment with a particular set of physico-chemical conditions, and with a particular array of organisms as neighbours. Organisms, as you have seen, can be finely adapted to a particular pH of soil or water, a particular food source, or a particular grazing regime. This fine-tuning is the result of the action of natural selection—which is where our story began.

OBJECTIVES FOR UNIT 25

After you have worked through this Unit, you should be able to:

- 1 Explain the meaning of, and use correctly, all the terms flagged in the text.
- 2 Interpret food chains or webs by stating the categories of the organisms in them. (SAQs 3 and 6)
- 3 Interpret energy flow diagrams and, given the appropriate data, work out assimilation, respiration and production values for the organisms in them. (SAQs 4, 5 and 6)
- 4 State the part played by different categories of organisms in the cycling of carbon, nitrogen, phosphorus and sulphur in ecosystems. (SAQ 6)
- 5 Show how the principle of energy flow and mineral cycling can be related to problems of human food production (SAQs 9 and 10)

- 6 Explain how human activities have altered the cycling of carbon, nitrogen, phosphorus and sulphur. Relate these alterations to the greenhouse effect, eutrophication and acid rain, and describe some of the problems that these may cause. (SAQ 7)
- 7 Construct life tables and survivorship curves from relevant data and interpret these by stating how mortality rates vary between stages. (SAQ 11)
- 8 Calculate k_{total} and k -values for a population from relevant data. (Experiment; SAQ 12)
- 9 Interpret graphs showing k_{total} and k -values by stating which is likely to be the key mortality factor and which are regulating mortality factors. Use data to suggest hypotheses about how these mortalities actually work (e.g. by altering the food supply). (SAQ 13)

ITQ ANSWERS AND COMMENTS

ITQ 1 (a) Up to the time of harvest, all cress *NPP* is transformed into new cress tissues: the seedlings *grow*, new cells are made and plant mass increases. If you ate the cress, some material would probably remain undigested and be lost as faeces. The rest would be digested, absorbed from your gut and either respired by your cells or converted into your own cell material (this would be *your* production). If the cress died before harvest, then it may be used as food by moulds (fungi) and bacteria. These organisms would convert some of the dead cress into their own cell materials and grow, and use some of it to fuel their respiration. The same would apply if you threw it on a compost heap.

(b) The one thing that does *not* happen on this island is an accumulation of annual *NPP* as new plant material (as in the saucer of cress seedlings) because you are told that the total mass of plants remains constant from year to year. So the *NPP* must in the end pass to animals that eat living plants and to animals or organisms such as fungi and bacteria in the soil that consume dead plant material. These plant and 'detritus' eaters will respire most of what they consume and digest; but some of the animal 'flesh' produced will be eaten by carnivores. Since the total mass of heterotrophs is constant, all the food consumed is balanced by the energy dissipated through respiration—and most of that respiration will be by the soil fungi and bacteria that decompose dead tissues.

Note: If you didn't manage to work much of this out, don't worry: the topics are discussed fully in the text that follows the ITQ.

ITQ 2 $2.9 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$; 96 %.

The total energy input is the sum of the values in the three dark boxes: solar energy trapped as *GPP* ($2.8 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$) + terrestrial insects and bait ($7.8 \times 10^2 \text{ kJ m}^{-2} \text{ yr}^{-1}$) + leaf litter from the banks ($3.3 \times 10^2 \text{ kJ m}^{-2} \text{ yr}^{-1}$) $\approx 2.9 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$. *GPP*, the input derived from plant photosynthesis, constitutes about 96 % of this total.

ITQ 3 $1.0 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$.

$$R = GPP - NPP = (2.8 \times 10^4 - 1.8 \times 10^4) \text{ kJ m}^{-2} \text{ yr}^{-1} \\ = 1.0 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

ITQ 4 $1.2 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$.

If the total biomass and amount of detritus in the ecosystem is constant, then total energy input (which you calculated for ITQ 2) will equal total energy output. In this case the total energy output is the sum of all the respiratory values, i.e.

$$(10\,000 + 700 + 2\,000 + 650 + 60 + 420 \\ + 3\,500 + X) \text{ kJ m}^{-2} \text{ yr}^{-1} \\ \approx (1.7 \times 10^4 + X) \text{ kJ m}^{-2} \text{ yr}^{-1}$$

$$\text{Total energy input} = 2.9 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

$$\text{So, } 2.9 \times 10^4 \approx (1.7 \times 10^4 + X) \text{ kJ m}^{-2} \text{ yr}^{-1}$$

$$X \approx (2.9 - 1.7) \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

$$\approx 1.2 \times 10^4 \text{ kJ m}^{-2} \text{ yr}^{-1}$$

ITQ 5 (a) Herbivores and detritivores: midge larvae feed on living plants and detritus (mixed up with decomposers). (b) First carnivores: young fish feed on the herbivorous zooplankton and midges. (c) First carnivores: leeches feed on midge larvae and, as you will see later, also on snails. (d) First and higher carnivores and also detritivores: notice from Figure 8 that detritus is their principal food (a consumption of $2\,000 \text{ kJ m}^{-2} \text{ yr}^{-1}$), but older fish also feed on the herbivorous midge larvae and zooplankton, on carnivorous young fish and leeches, and also on terrestrial insects (some of which are likely to be carnivores). (e) Detritivores: snails feed on dead leaves and other detritus (plus the decomposers attached to this material).

ITQ 6 (a) $k_3 = 0.429$; $k_4 = 0.028$; $k_5 = 0.222$.

(b) $k_{\text{total}} = \log N_0 - \log N_5 = \log 72/9 = 0.903$

Alternatively, k_{total} can be found by adding $k_1 \dots k_5$:

$$k_1 + k_2 + k_3 + k_4 + k_5 = 0.150 + 0.074 + 0.429 \\ + 0.028 + 0.222 \\ = 0.903$$

ITQ 7 1.7

98 % mortality from 100 eggs laid would leave two survivors. Hence N_A is 2 and N_B is 100.

$$k_{\text{total}} = \log \frac{N_B}{N_A} = \log \frac{100}{2} \approx 1.7$$

SAQ ANSWERS AND COMMENTS

SAQ 1 (a) A moorland *ecosystem* contains grassland, scrub and stream *habitats*.

(b) Highland streams are a *habitat* for trout and salmon.

(c) A domestic cat harbours a *population* of fleas, *Ctenocephalides felis*, in its fur.

(d) Ladybirds are members of the predator *community* that feeds upon *populations* of greenfly, reducing their numbers.

(e) The grassland *ecosystem* of the Serengeti in Africa is grazed by a *community* of large herbivores including wildebeeste, zebra, topi and buffalo.

SAQ 2 (a) False. Carnivores eat other animals, so they obtain energy in a chemical form (as organic molecules) and are, therefore, heterotrophs.

(b) True. Both categories use 'food' (organic matter) as a source of energy. 'Consumer' is a general term for animals, and 'decomposer' is a general term for micro-organisms (including bacteria and fungi) that feed on dead organic matter (dead organisms and their waste products). The difference between them is that consumers usually take food into their bodies and break it down (digest it) there; whereas decomposers usually break down food outside their bodies or cells (many are single-celled) and then absorb the breakdown products from the outside.

(c) True. See Section 2.1.

(d) False. Energy flows through an ecosystem. Some of it may be stored (as biomass or dead organic material in the soil or sediments) but most is usually dissipated as heat through respiration. There is no recycling. See Sections 2.2 and 2.3.

(e) False. Although true for many detritivores some depend almost wholly on animal remains and others on plant litter or detritus. So some detritivores are not really omnivorous.

(f) False. Production is the term used for heterotrophs to describe the residue of assimilated energy left after respiration, i.e. production = assimilation – respiration (see Section 2.2). It is equivalent to the *NPP* of plants. So production *may* be manifested as an increase in biomass, but more usually it is consumed by the next trophic level or, after death, transferred to the decomposers (see, for example, Figure 7). If annual production of a population were to equal increase in population biomass, it would imply that no members of the population died or were eaten! This is a possible but unlikely state of affairs for natural populations.

(g) False. Consumption by herbivores is one of the possible fates of *NPP* in an ecosystem, but this rarely accounts for more than 40% of it. Storage, for example as woody biomass, or transfer to the decomposers as litter or detritus is the usual fate.

SAQ 3 (a) *Herbivores*: limpets (i) mussels (v) and flat periwinkles (vi); you should have recalled from the Thames study that diatoms are plants. *First carnivores*: barnacles (iv) (assuming the zooplankton is herbi-

vorous), dogwhelks (ii) (when feeding on mussels), turnstones (viii) (when feeding on limpets and periwinkles). *Higher carnivores*: dogwhelks (ii) (when feeding on barnacles), turnstones (viii) (when feeding on dogwhelks). *Detritivores*: crabs (iii) and gulls (vii). *Decomposers*: no decomposers are listed under (i)–(viii).

(b) Possible food chains are:

mussels → dogwhelks → turnstones

diatoms (on seaweeds) → flat periwinkles → turnstones

diatoms (on rocks) → limpets → turnstones

So there are several food chains present. A food web would be a better description of the system (note how diatoms and turnstones appear in more than one chain).

SAQ 4 Recall that food assimilated, A = respiration, R + production, P (Section 2.2). Using the equation $A = R + P$, the values can be calculated by addition or subtraction (all in $\text{kJ m}^{-2} \text{yr}^{-1}$). For example, for animal U (which were voles), the value required (a) is assimilation. In this case, $A = (68 + 2) \text{kJ m}^{-2} \text{yr}^{-1} = 70 \text{kJ m}^{-2} \text{yr}^{-1}$.

The other values, all in $\text{kJ m}^{-2} \text{yr}^{-1}$, are given below and, for interest, the organisms to which these data refer are shown in brackets after each answer.

(a) 70 (voles)

(b) 26 (grasshoppers)

(c) 13.8 (sparrows)

(d) 15.3 (squirrels)

(e) 48 (bleak, growing slowly because of over-crowding)

(f) 626 (African antelopes)

SAQ 5 (a) $4 \times 10^4 \text{kJ m}^{-2} \text{yr}^{-1}$.

Using the relationship $GPP = NPP + R$,

$$\begin{aligned} x &= (9 \times 10^4) - (5 \times 10^4) \text{kJ m}^{-2} \text{yr}^{-1} \\ &= 4 \times 10^4 \text{kJ m}^{-2} \text{yr}^{-1} \end{aligned}$$

(b) As sunlight leads to box V, this box must represent plants, i.e. primary producers. Box Z has arrows to it from all the others, so this must represent decomposers (plus detritus).

Therefore, box W represents herbivores, box X first carnivores and box Y higher carnivores.

(c) There is a net export of $10 \times 10^3 \text{kJ m}^{-2} \text{yr}^{-1}$.

Since this system is in a steady state (because total biomass and detritus are constant), the total energy input must equal the total energy output. If the *GPP* is equal to overall respiration, then the system will be self-contained (i.e. primary production is the sole energy input); if the *GPP* is less than overall respiration, then there must be a net energy import (of organic matter from outside the system); and if the *GPP* is greater than overall respiration, there must be a net energy export (of organic matter leaving the system). In this case, the latter is true: $GPP = 90\,000 \text{kJ m}^{-2} \text{yr}^{-1}$, and overall respiration in $\text{kJ m}^{-2} \text{yr}^{-1}$ is

$$50\,000 + 10\,300 + 1\,300 + 60 + 18\,000 = 79\,660$$

So there must be a net export of $(90\,000 - 79\,660) \text{ kJ m}^{-2} \text{ yr}^{-1} = 10\,340 \text{ kJ m}^{-2} \text{ yr}^{-1}$. This will include excess detritus that the decomposers did not break down, and an amount of decomposer organisms equivalent to decomposer production ($2\,000 \text{ kJ m}^{-2} \text{ yr}^{-1}$), since the average biomass of decomposers is constant.

SAQ 6 The *essential* organisms are (i), (iii) and (v).

Green plants are necessary to take up inorganic nitrogen and convert it to organic nitrogen—the only form in which most heterotrophs can obtain it. Decomposers are the only organisms able to convert organic nitrogen back to an inorganic form (NH_4^+). Nitrogen-fixing bacteria are essential (at least in unmanaged ecosystems) for replacing the nitrates lost through leaching and denitrification. This happens after the death of free-living nitrogen-fixers through the activities of decomposers and nitrifying bacteria. In managed ecosystems, nitrogen fertilizers may be applied instead of depending on nitrogen-fixing bacteria.

Herbivores are not essential because even in their absence, organic nitrogen passes from plants to decomposers when plants die. Denitrifying bacteria actually cause a leak in the nitrogen cycle when they convert nitrates to molecular nitrogen or nitrogen oxides; so they are certainly not essential for the operation of the cycle.

SAQ 7 (a) (i) Burning coal interferes with the cycling of carbon, nitrogen and sulphur because coal (a fossil fuel) releases carbon dioxide, oxides of nitrogen and sulphur dioxide when burnt. This represents a shift of these elements from a geological reservoir to the atmosphere.

(ii) Flushing the lavatory after using it interferes with the cycling of nitrogen and phosphorus. The organic wastes flushed down the lavatory contain much nitrogen and phosphorus. Instead of being decomposed by soil decomposers, these are decomposed by bacteria in sewage works to inorganic ions, which pass into freshwaters with treated sewage effluent. This shifts inorganic nitrogen and phosphorus from soil to water.

(iii) Clearing and ploughing interfere with the cycling of carbon and nitrogen (and possibly sulphur). It leads to oxidation of soil organic matter and a release of carbon dioxide into the atmosphere. If the cleared trees were burnt, this would increase this transfer. The disturbance involved is very likely to increase leaching of soil nitrates and, depending on the type of soil, there may also be increased leaching of sulphate. Because of its immobility in soil, phosphate ions are unlikely to be lost by leaching.

(b) (i) Burning coal contributes to the greenhouse effect (Section 3.1) through the release of carbon dioxide and nitrogen oxides, and to acid rain (Section 3.4) through the release of nitrogen oxides and sulphur dioxide.

(ii) Flushing the lavatory after using it contributes to eutrophication (Sections 3.2 and 3.3) because the soluble nitrogen and phosphorus salts released into water stimulate the growth of algae.

(iii) Clearing and ploughing contribute to the green-

house effect and to eutrophication (through the leaching of nitrates).

SAQ 8 Clover is a legume with root nodules containing nitrogen-fixing bacteria, so when this crop was grown and ploughed in, there was an addition of nitrogen. This promoted the subsequent growth of the wheat, a crop that requires high levels of nitrogen for good growth. The roots and hay fed to stock during the winter resulted in the manuring of the field by the stock, so the mineral salts were conserved and made available by decomposition ready for the sowing of barley in the spring. These farmers either used the straw for their beasts, and then distributed manure onto the fields and ploughed it in, or ploughed in straw after the harvest. All that they removed from their land was the grain of the two cereal crops and milk, meat and other products of their stock.

SAQ 9 The two most feasible ways are to:

(a) Catch the anchoveta and use these small fish as food. They are the first carnivores and eating them puts people into the category of second carnivores.

(b) Dig up the guano from the islands and use it as phosphate fertilizer to promote the growth of crops in areas where the soil is deficient in phosphorous. People eating these crops would be in the category of herbivores, using the Sun's energy efficiently. In the sea ecosystem, the guano birds are top carnivores but they make phosphate from the sea available for use on land.

In fact, in the past, the guano was mined and sold as fertilizer; but more recently, anchoveta have been caught in large numbers and then converted to fish meal to feed poultry, pigs and cattle, *not* people. The reduction in the numbers of anchoveta led to mass mortalities of guano birds, so supplies of phosphate fertilizer have ceased to be available.

SAQ 10 (a) False. If pre-reproductive mortality of the offspring generation equals the fecundity of the parent generation, then there will be no survivors of the offspring generation. The population will therefore decrease in size and so not be stable.

(b) False. They do sometimes but not always: see Figure 21b.

(c) False. They may be; but often they are catastrophic factors related to weather and totally unrelated to density.

(d) False. Usually some k -values change, resulting in changes in the population.

(e) True. They kill a higher proportion of a more dense (crowded) population and a lower proportion of a less dense population and, consequently, tend to bring the numbers towards an intermediate value.

(f) False as a general statement. If an efficient agent is found then biological control is more efficient and usually much less costly than chemical control; but it is not always possible to find a suitable agent.

(g) False. A mortality that kills the same number of individuals each year, irrespective of the population density is obviously density independent.

SAQ 11

	(a) number	(b) life table
eggs laid by female moth	200	100
caterpillars surviving the winter	16	8
caterpillars surviving <i>Cyzenis</i> attack	15	7.5
caterpillars surviving other parasites	13.5	6.75
caterpillars surviving disease	11	5.5
pupae surviving predators in the soil	2.5	1.25
pupae surviving <i>Cratichneumon</i> attack and becoming adults	2	1

SAQ 12 The calculation can be laid out thus:

	number	k-values
eggs laid by female moth	200	
caterpillars surviving the winter	16	$k_1 = 1.097$
caterpillars surviving <i>Cyzenis</i> attack	15	$k_2 = 0.028$
caterpillars surviving other parasites	13.5	$k_3 = 0.046$
caterpillars surviving disease	11	$k_4 = 0.089$
pupae surviving predators in soil	2.5	$k_5 = 0.643$
pupae surviving <i>Cratichneumon</i> attack and becoming adults	2	$k_6 = 0.097$
generation pre-reproductive mortality, $k_{\text{total}} = \text{sum of } k\text{-values} = 2.00$		

SAQ 13 (a) The values of k_s vary in much the same way as k_{total} (except in 1973), so starvation is probably the key mortality factor.

(b) No. None of the k -values shows obvious variations in the opposite direction to k_{total} . This population shows enormous swings in density suggesting that any regulating factor is very weak.

SAQ 14 (a) This is basically true, although it is not usually as easy to see a species' niche as it is on a rocky shore.

(b) False. Experiments are needed, such as the one in which Connell removed *Balanus* to find out if it limited the distribution of *Chthamalus*.

(c) True. This also occurs with *Balanus* and *Chthamalus*, and with the different species of seed-eating rodents in the deserts of the southwest USA.

(d) False. The communities of rocky sea shores and other habitats may vary from place to place.

(e) False. Although human activities are responsible for some major changes in communities, such as those which followed the eradication of the rabbit in Britain by myxomatosis, not *all* such changes are due to humans.

(f) False. Cyclical regeneration causes local changes in the composition of a climax community.

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Figure 31: Bowers, M. A. and Brown, J. H. 'Body Size and Co-Existence in Desert Rodents: Change or Community Structure' vol. 63, no. 2, *Ecology*, 1982, Ecological Society of America.

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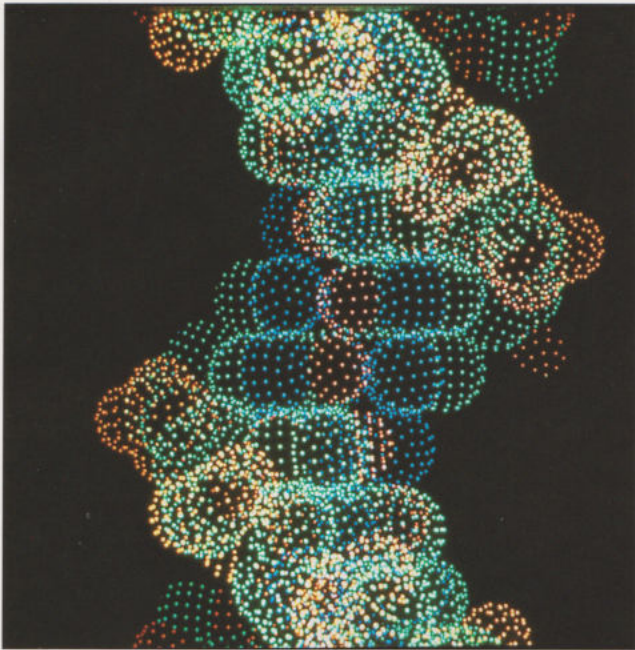


PLATE 1 Side view of DNA, with the individual atoms represented as dot-covered spheres. Carbon is green, oxygen is red, nitrogen is blue and phosphorus is yellow. The sugar-phosphate backbone on the far side of the structure is not shown.

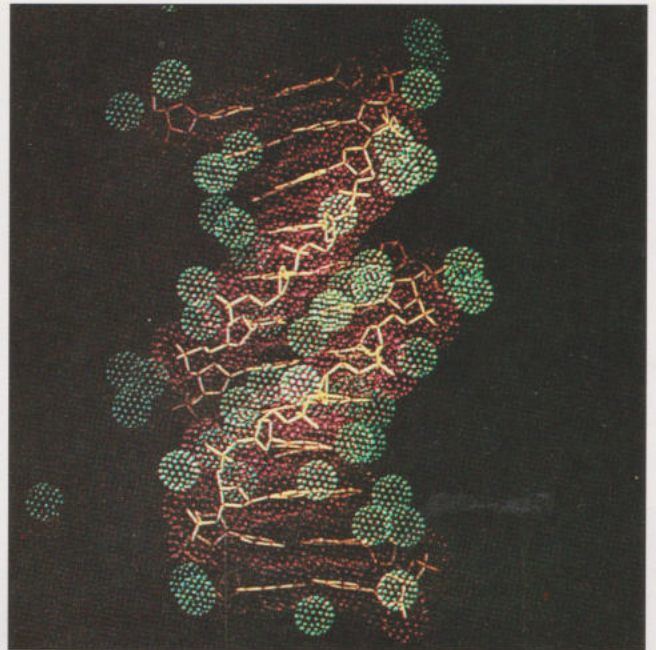


PLATE 2 Model of DNA. The skeleton is yellow with the surface indicated by red dots. The green dots show the location of the water molecules that would be found associated with the DNA in the nucleus.



PLATE 3a Bracken, *Pteridium aquilinum*, a fern that is common in Britain and widely distributed throughout the world.



PLATE 3b Common reed, *Phragmites australis*, a grass that grows in water and damp places and is common throughout the world.



PLATE 4 Roach, *Rutilus rutilus*, in an aquarium.



PLATE 5 Typical mine in a holly leaf.



PLATE 6 Holly leaf miner.



PLATE 7 A mine in a holly leaf torn open by a bird. (The pin-head indicates size.)



PLATE 8 Emergent hole of a parasitic wasp, the empty pupal case of the fly and the remains of the parasitic wasp.



PLATE 9 Emergent hole of the adult miner (a) with triangular flap intact, (b) with flap removed, and (c) with top surface of the leaf cut away to expose pupal case.



PLATE 10 Cottony cushion scale, *Icerya purchasi*, on a citrus stem.



PLATE 11a Lullington Heath, Sussex, on 23 March 1954.



PLATE 11b Lullington Heath, Sussex, on 21 February 1967.



PLATE 12a Old Winchester Hill, Hampshire, on 10 August 1954.



PLATE 12b Old Winchester Hill, Hampshire, on 13 August 1956.



PLATE 13a View of Chiltern Hills (Aston Rowant) with Nature Reserve and Motorway (M40).



PLATE 13b Aerial view of part of Aston Rowant Nature Reserve showing the fence to keep out rabbits, small ungrazed plots and meadow heavily grazed by sheep.

PLATE 13c Rockrose, *Helianthemum chamaecistus*, plants grazed by rabbits.

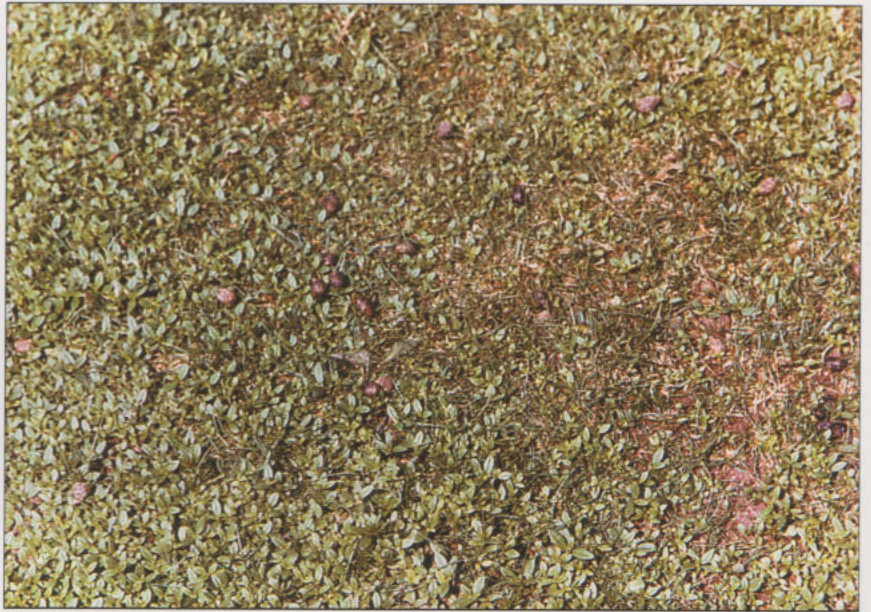


PLATE 13d Rabbit warren showing patches of stinging nettles, *Urtica dioica*.



PLATE 13e Ant-hill in a lightly grazed meadow in summer.



PLATE 13f Area with ragwort plants, *Senecio jacobaea*, in summer.



PLATE 13g Ungrazed area with scrub growing up in summer.





PLATE 14a Clustered bellflower, *Campanula glomerata*, flowers.



PLATE 14b Rockrose, *Helianthemum chamaecistus*, flower.



PLATE 14c Marjoram, *Origanum vulgare*, in flower.



PLATE 14d Scabious, *Scabiosa columbaria*, flower.



PLATE 14e Pyramidal orchid, *Anacamptis pyramidalis*, flowers.



PLATE 14f Greater knapweed, *Centaurea scabiosa*, flower with a hoverfly (order Diptera, family Syrphidae).



PLATE 14g Wild carrot, *Daucus carota*, in flower with a burnet moth, *Zygaena filipendulae* (order Lepidoptera).